UNIVERSITÉ DU QUÉBEC À MONTRÉAL

L'HÉTÉROGÉNÉITÉ PAYSAGÈRE CONTEMPORAINE DU SUD-OUEST DE LA FORÊT BORÉALE QUÉBÉCOISE EN LIEN AVEC QUATRE FAMILLES DE VARIABLES EXPLICATIVES

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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JUIN 2015

REMERCIEMENTS

Ce projet de thèse s'est amorcé il y a bien longtemps (quelques années après la première édition du Manuel de Foresterie, publié en 1996), suite à une proposition de Yves Bergeron, auquel s'est rapidement associée Sylvie Gauthier. Yves et Sylvie, tous deux visionnaires, m'ont convaincu de la pertinence d'étudier le rôle des pertubations (naturelles et humaines) en lien avec le climat et le milieu physique dans la structuration des paysages boréaux de l'ouest du Québec. Par la suite, Yves et Sylvie m'ont suivi tout au long de cette épopée, en me revenant régulièrement avec leurs analyses, corrections de textes et encouragements; je leur dois en grande partie ce doctorat. Je les remercie également d'avoir accepté mes nombreuses digressions vers d'autres projets auxquels, peut-être à tort, j'ai accordé temporairement priorité. Il me fut difficile de distinguer l'employé de l'État et l'étudiant qui, quelque part, devait trouver la confiance du doctorant pour foncer vers le but final de l'obtention du diplôme (9 décembre 2014). Ce but n'aurait pu être atteint sans le soutien de mes patrons passés et actuel (René Doucet, Robert Jobidon, Agathe Cimon, Michel Campagna) et l'autorisation du ministère des Ressources naturelles d'utiliser les impressionnantes bases de données (placettes d'inventaire forestier, cartes forestières...), accumulées au cours des 40 dernières années, fruit du labeur de nombreux forestiers anonymes que nous remercions sincèrement. Dans les premières phases du présent doctorat, Marie-Josée Fortin et Louis Bélanger ont apporté des commentaires pertinents à son orientation. Par ailleurs, ce projet n'aurait pu être réalisé sans l'appui inconditionnel de mon « équipe de soutien » composée de mon épouse (Line Couillard), de notre garçon (Étienne), de sa conjointe (Olivia) et, depuis peu et sans qu'il puisse le verbaliser, de notre petit-fils Arthur. Par ailleurs, tous les coauteurs des chapitres m'ont été d'une aide indispensable. Daniel Borcard a été un fidèle conseiller en écologie numérique et, sans ses enseignements, imprégnés de ceux de Pierre Legendre, ce doctorat n'aurait pu reposer sur l'écologie numérique. Patrice Tardif est intervenu sur des aspects reliés à la mathématique. Rémi St-Amant, du Service canadien des forêts, nous a guidés relativement au logiciel BioSim (climat). Jean Noël, Denis Hotte et Véronique Poirier ont été d'une aide régulière en géomatique et en traitement de bases de données. Les trois chapitres constituant le travail ont bénéficié des commentaires et de la traduction anglaise de mon « comité de lecture », formé de Yan Boucher, Karen Grislis, Paul Jasinski, Jason Laflamme, Del Meidinger, Germain Mercier, Héloise Rheault et Denise Tousignant. Un merci spécial aux dames du secrétariat de l'UQAM (Lucie Brodeur, Élisabeth Lindsay) qui m'ont permis, dans les dernières phases du doctorat, de satisfaire les nombreuses exigences administratives et d'en organiser la soutenance. Merci également aux collègues du Ministère de ressources naturelles (MRN) pour leurs encouragements. Les membres de l'équipe de classification écologique des forêts du Québec du MRail N (voir Saucier et al. 2009, seconde édition du Manuel de Foresterie) ont influencé les orientations données à ce projet; comme équipe on se devait d'ajouter à notre réflexion une composante touchant les perturbations naturelles et humaines et ce projet va dans ce sens. Enfin, merci à Nathalie Langlois pour la mise en forme du document.

AVANT-PROPOS

Cette thèse se compose d'une introduction générale, de trois chapitres et d'une conclusion générale. Les trois chapitres sont présentés sous forme d'articles scientifiques publiés ou engagés dans le processus de publication. J'ai réalisé la grande majorité des analyses, en plus de la rédaction de l'ensemble de la thèse. Le premier chapitre, intitulé *Drivers of contemporary landscape vegetation heterogeneity in the Canadian boreal forest: integrating disturbances (natural and human) with climate and physical environment*, a été accepté et sera publié en 2015 par la revue *Ecoscience.* Les coauteurs en sont Sylvie Gauthier et Yves Bergeron, ainsi que Daniel Borcard, Patrice Tardif et Denis Hotte. Sylvie Gauthier et Yves Bergeron ont proposé le sujet de cette recherche et ses grandes orientations. Ils en ont supervisé les travaux jusqu'à la publication. Daniel Borcard et Patrice Tardif ont été d'indispensables conseillers en écologie numérique. Denis Hotte a contribué à l'analyse des données.

Le deuxième chapitre, intitulé *A new approach to ecological land classification for the Canadian boreal forest that integrates disturbances,* a été publié en janvier 2014 dans la revue *Landscape Ecology.* Les coauteurs en sont Sylvie Gauthier et Yves Bergeron, ainsi que Daniel Borcard et Jean Noël. Sylvie Gauthier, Yves Bergeron et Pierre Grondin ont développé conjointement la problématique et les hypothèses de cette étude. Daniel Borcard a pousuivi son rôle de conseiller en écologie numérique; Jean Noël a contribué à l'analyse des données. Le premier et le second article sont en lien avec un mémoire publié à la Direction de la recherche forestière du Ministère des ressources naturelles du Québec (MRN) (Grondin et al. 2007).

Le troisième chapitre, intitulé *Comparison of natural and managed landscapes, and reference conditions for ecosystem management in a large portion of the eastern Canadian boreal forest* sera soumis à la revue *Forest ecology and management* en

2015. Les coauteurs en sont Sylvie Gauthier, Yves Bergeron, Patrice Tardif, Jean Noël et Denis Hotte. L'article se situe dans la poursuite de travaux publiés par Sylvie Gauthier, Yves Bergeron et Alain Leduc; Pierre Grondin a utilisé ces connaissances et les a appliquées à l'ensemble du territoire d'étude selon deux niveaux de perception : l'unité homogène de végétation et la combinaison végétation potentielle-stade évolutif. Patrice Tardif a été un efficace conseiller en mathématiques; Jean Noël et Denis Hotte ont contribué à l'analyse des données. Un mémoire de la direction de la recherche forestière du MRN traite du sujet abordé dans cet article (Grondin et al. 2010).

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RÉSUMÉ GÉNÉRAL

Ce projet propose un modèle d'analyse de l'hétérogénéité forestière contemporaine d'un territoire vaste (175 000 km^2) et varié de la forêt boréale québécoise. Il s'insère dans le contexte de la gestion des forêts du Québec s'appuyant sur les principes de l'aménagement écosystémique. Il a pour but de mieux connaître les processus qui sont à l'œuvre sur le territoire d'étude, cette connaissance conditionnant l'efficacité des politiques d'aménagement mises en place. Nous nous intéressons plus spécifiquement à la complexité des paysages forestiers boréaux définie par les gradients écologiques le long desquels la végétation et ses variables explicatives sont modulées. Quatre familles de variables explicatives sont considérées : le climat, les perturbations naturelles, le milieu physique et les perturbations humaines. Notre objectif est de définir, sous différents angles, ces familles de variables, leur chevauchement le long de gradients écologiques, leur distribution régionale et leur contribution à la diversité des paysages forestiers. Cette approche s'inscrit dans la lignée de deux paradigmes qui se sont succédé au cours des 100 dernières années : le premier axé sur des paysages à l'équilibre et montrant beaucoup de constance d'une perturbation à l'autre (*balance of nature*) et le second orienté vers des paysages en équilibre dynamique et composés d'une mosaïque de peuplements dont la composition, l'âge et les structures sont variés (*patch dynamics*). Cette thèse aborde plus spécifiquement l'hétérogénéité des paysages du territoire d'étude sous trois aspects :

1- les gradients écologiques, les structures spatiales (cartes) et l'estimation de l'importance des quatre familles de variables environnementales dans la variation de la végétation décrite selon trois thèmes : les espèces forestières, les types forestiers et les végétations potentielles-stades évolutifs,

2- l'expression dans l'espace des liens entre la végétation et ses variables explicatives, telle que manifestée par des entités géographiques relativement similaires, au regard de la végétation et de leurs variables explicatives (unités homogènes de végétation),

3- et la comparaison de paysages formés par les processus naturels avec les paysages aménagés formés par les mêmes processus, auxquels s'ajoutent les activités anthropiques.

Dans le premier chapitre, l'hétérogénéité paysagère du territoire d'étude a été caractérisée à partir de plusieurs sources de données du ministère des Ressources naturelles du Québec (MRN), notamment les districts écologiques (cellules territoriales d'une superficie moyenne de 200 km^2), les inventaires forestiers et écologiques ainsi que des cartes forestières, tous réalisés ou élaborés au cours des

30 dernières années. Les résultats obtenus de la compilation de ces données démontrent que l'hétérogénéité des paysages s'exprime par des changements de végétation synchrones avec ceux des variables explicatives présentes le long des gradients écologiques. Cette hétérogénéité est donc structurée ou ordonnée, par opposition à une hétérogénéité sans lien avec les gradients écologiques. Ainsi, deux types de gradients écologiques et de structures spatiales caractérisent le territoire. Le premier, le gradient latitudinal (nord-sud), caractérise deux thèmes de végétation : les espèces forestières, et les végétations potentielles-stades évolutifs. Ce gradient est surtout le reflet des modifications qui surviennent dans les perturbations naturelles et le climat. Le second type, le gradient latitudinal oblique (du sud-est vers le nord-ouest), caractérise le troisième thème, celui des types forestiers. Ce gradient est également le reflet des modifications qui surviennent dans les perturbations naturelles et le climat, mais le milieu physique est plus important que dans les deux premiers thèmes. Cela dit, peu importe le thème de végétation, ce sont les combinaisons de plusieurs familles de variables explicatives qui expliquent le mieux la répartition de la végétation, notamment celles qui impliquent les trois familles naturelles : les perturbations naturelles, le climat et le milieu physique. Dans l'ensemble (variation totale), les perturbations humaines expliquent toujours une proportion moindre de variation que les familles de variables naturelles.

En utilisant les mêmes sources de données que dans le chapitre précédent, nous nous sommes intéressés, au deuxième chapitre, à segmenter ce territoire hétérogène, mais cependant structuré et organisé, selon des unités spatiales relativement homogènes définies par une végétation et des familles de variables explicatives spécifiques. L'hétérogénéité paysagère a été caractérisée selon trois échelles ou niveaux de perception. Au niveau le plus fin, 14 unités se succèdent le long des gradients écologiques et trois types d'unités se distinguent sur la base des processus écologiques. Le premier type est associé aux épidémies de tordeuse des bourgeons de l'épinette (portion sud), le second, aux peuplements de début de succession (pinèdes grises et tremblaies) relativement jeunes (surtout dans la portion centrale) et le troisième, aux peuplements de fin de succession (principalement des pessières noires) relativement âgés (prédominant dans la portion nord). Enfin, bien que les perturbations humaines soient présentes sur le territoire depuis plus de 100 ans, la variation de la végétation qui leur est associée est moindre que celle qui est propre aux familles naturelles. Par contre, ces activités ont suffisamment influencé la dynamique paysagère pour affecter le contenu de plusieurs unités homogènes et parfois même modifier leurs limites. Par ailleurs, peu importe le niveau de perception étudié, la variation de la végétation est essentiellement contrôlée par une combinaison de familles de variables explicatives plutôt que par des familles prises individuellement. Afin de positionner l'approche des unités homogènes le long de la séquence évolutive des classifications écologiques du territoire, nous avons appliqué les concepts proposés par divers auteurs (e.g. végétation, végétation et milieu physique) à notre territoire. Les résultats obtenus montrent beaucoup de convergence entre les classifications, ce qui est conséquent avec le synchronisme et le chevauchement des variables descriptives (végétation) et explicatives le long des gradients écologiques.

Dans le troisième chapitre, nous nous sommes intéressés à comparer les unités homogènes décrites au chapitre précédent sur la base de leur paysage naturel (sans intervention anthropique) et de leur paysage actuel (principalement aménagé). Le défi porte sur une définition du paysage naturel pour les unités homogènes touchées par les activités anthropiques. Pour ce faire, nous avons utilisé une méthode intégrant le cycle de feu, la structure d'âge du paysage et la modélisation de la dynamique forestière. Cette méthode considère également la variabilité spatiale actuelle du cycle de feu, la variabilité temporelle contemporaine (avant et après 1850) et, jusqu'à un certain point, la variabilité plurimillénaire. Les résultats suggèrent que quelques paysages aménagés se situent en dehors des limites de leur variabilité naturelle, principalement en ce qui a trait aux forêts de plus de 100 ans, mais également pour ce qui est de la composition forestière (enfeuillement).

Ayant en vue d'améliorer la mise en œuvre de l'aménagement écosystémique du territoire d'étude par une meilleure connaissance des processus qui y sont à l'oeuvre, cette thèse a permis d'expliquer l'hétérogénéité des paysages sur la base de l'intégration de quatre familles de variables explicatives (climat, perturbations naturelles, milieu physique, perturbations humaines). Pour atteindre ce résultat, nous nous sommes intéressés à répondre à trois questions. Tout d'abord, quelle est la complémentarité des familles de variables explicatives considérées dans le développement et le maintien de l'hétérogénéité des paysages définis selon divers thèmes de végétation (espèces forestières, types forestiers, végétations potentielles-stades évolutifs)? Ensuite, comment la végétation et les diverses familles concourent-elles à la formation d'unités relativement homogènes définies selon divers niveaux de perception? Enfin, quel est l'écart entre les paysages naturels et les paysages aménagés en considérant les unités homogènes (échelle spatiale) ainsi que la combinaison des végétations potentielles et des stades évolutifs (échelle du peuplement)?

Le modèle d'analyse de l'hétérogénéité proposé dans cette étude tend vers la définition du paysage naturel de chacune des unités de territoire retenues (14 unités homogènes de végétation). Chacun des paysages, décrit par une variabilité naturelle contemporaine et plurimillénaire, peut être considéré comme l'expression optimale de la biodiversité sur laquelle pourrait se baser l'aménagement écosystémique. Le pas suivant serait de lier la description des paysages présentés dans cette étude (végétation contemporaine), avec la description issue de la paléoécologie. Cette discipline permet de dresser l'histoire holocène de la végétation, des feux et du climat à partir d'archives sédimentaires (ex. sédiments lacustres) dans le but de définir une variabilité naturelle plurimillénaire. Alors, la manière de coupler ces deux approches de description des paysages et de leur variabilité représente un défi intéressant. Un second objectif possible serait de comparer la variabilité passée et actuelle avec celle anticipée sous l'effet des changements climatiques.

Mots-clés : intégration de la végétation et de ses variables explicatives, hétérogénéité spatiale, analyses de redondance, aménagement écosystémique, forêt boréale, paysage naturel

INTRODUCTION GÉNÉRALE

Cette étude s'inscrit dans le contexte de la mise en oeuvre de l'aménagement écosystémique, c'est-à-dire un aménagement qui vise le maintien de la biodiversité ainsi que la viabilité des écosystèmes, sur le court et le long terme (Swanson et al. 1994, Landres et al. 1999). Pour y parvenir, l'aménagement écosystémique a comme objectif de réduire l'écart entre les paysages naturels et les paysages aménagés (Gauthier et al. 2008). À cet égard, les paysages naturels (peu ou pas touchés par les activités anthropiques), de par leur résilience face aux processus écologiques plurimillénaires, sont considérés comme la réponse la plus susceptible de garantir la durabilité de nos écosystèmes dans un contexte de changements climatiques. Ces paysages constituent donc les états de référence vers lesquels on souhaite amener les paysages aménagés (modifiés par les activités anthropiques) (Boucher et al. 2011).

Les concepts et les connaissances liés aux processus écologiques qui créent et entretiennent l'hétérogénéité des paysages intéressent les écologistes depuis fort longtemps. « Among the earliest and most persistent concepts in ecology, under various pseudonyms, were homogeneity and its antonym, heterogeneity ». Les pseudonymes dont il est question dans cet énoncé de McIntosh (1991) correspondent aux divers paradigmes explicatifs des paysages forestiers, paradigmes qui se sont succédé depuis presque un siècle, à l'exemple de la « *balance of nature* » et de la « *patch dynamics* » (Wu et Loucks 1995). Les versions successives de ces paradigmes, au lieu de détruire les précédentes, ont constitué des apports complémentaires d'une réalité complexe, allant dans le sens d'une couverture plus vaste et plus complète des phénomènes en jeu. Toutefois, ce développement manquait jusqu'à maintenant d'une vision intégrative et d'outils d'analyse de l'hétérogénéité des paysages naturels et aménagés qui auraient rendu leur conceptualisation, leur description et leur aménagement de plus en plus cohérents et englobants.

Le paradigme du déterminisme de la dynamique paysagère

Dans une première période (1910-1980), les paysages étaient perçus comme étant relativement stables et dans un état d'équilibre (DeAngelis et Waterhouse 1987, Rohde 2005). L'altitude et le drainage étaient les principales variables qui déterminaient la séquence des assemblages floristiques (végétations potentielles) caractérisant les toposéquences (Blouin et Berger 2005). Un même type de milieu physique (ex. : till de drainage mésique) était fortement associé à une seule végétation potentielle (Jurdant et al. 1977). Par exemple, les tills mésiques du domaine de la sapinière à bouleau blanc étaient essentiellement occupés par des peuplements composant la série dynamique de la sapinière à bouleau blanc. Les connaissances sur les perturbations naturelles relatives à chacun des milieux physiques se limitaient à des schémas de la dynamique forestière illustrant l'évolution des forêts en fonction de la tolérance à l'ombre des espèces forestières (Clements 1916, Blouin et Grandtner 1971, Frelich et Reich 1995, White et al. 1999). Ces connaissances qualitatives sur la dynamique forestière étaient utilisées à plusieurs fins, notamment pour caractériser la biodiversité d'un territoire et pour définir des scénarios sylvicoles. La végétation actuelle était cartographiée de façon à la distinguer de la végétation potentielle (Blouin et Grandtner 1971, Jurdant et al. 1977, Gerardin et Ducruc 1990). L'hypothèse était que les peuplements composant la première de ces cartes (végétation actuelle) évolueraient vers ceux composant la seconde (végétation potentielle) et, qu'à moins d'imprévu, les espèces et les types forestiers de fin de succession devraient se maintenir dans le temps. Les perturbations naturelles étaient considérées comme externes à la dynamique des écosystèmes (facteur exogène). Elles étaient rares et accidentelles. Tout au plus, ces dernières replaçaient-elles les peuplements le long des trajectoires successionnelles des séries évolutives et la chronoséquence menait invariablement vers des peuplements de fin de succession. La dynamique de succession semblait inévitable : la pessière noire brûlait, la forêt de pin gris s'installait et, avec le temps, la forêt d'épinette noire reprenait sa place (Frelich et

Reich 1995, Lesieur et al. 2002, Lecomte et Bergeron 2005). Finalement, le paysage à l'équilibre, notamment soutenu par le concept de la « *balance of nature* », possédait les caractéristiques suivantes : 1- le maintien, après perturbation, des espèces (végétales et fauniques) et des peuplements ainsi que de tout autre élément d'intérêt relatif à la biodiversité, 2- une dynamique forestière similaire d'une perturbation à une autre, 3- une proportion relativement constante de la combinaison de peuplements et de stades évolutifs d'une perturbation à l'autre, 4- et une répartition des superficies par classe d'âge caractérisée par une décroissance régulière des jeunes peuplements vers les peuplements âgés (White et al. 1999). Plusieurs systèmes de classification écologique ont été développés en lien avec ce concept. Ces systèmes visaient à délimiter des entités (patterns) sur la base de la végétation et du climat (Rowe 1972), ou en tenant compte de la végétation, du climat et du milieu physique (Jurdant et al. 1977). La compréhension des paysages des écologistes de cette période s'apparentait à celle de la niche écologique (Hutchinson 1957).

Le paradigme de l'équilibre dynamique des paysages face aux perturbations

Si la première période a vu la prépondérance du paradigme du déterminisme de la dynamique paysagère, la seconde (1970 et plus) a été orientée vers une perception des paysages en état d'équilibre dynamique, c'est-à-dire davantage influencés par les perturbations naturelles (Watt 1947, Daubenmire 1968, Heinselman 1973, Holling 1973, Rowe et Scotter 1973, White 1979). Ces dernières étaient maintenant considérées comme un acteur de premier plan dans la création et le maintien de l'hétérogénéité des paysages (Heinselman 1981, Payette 1992, Wu et Loucks 1995, Turner et al. 1993, White et al. 1999). Les feux étaient un élément-clé de la résilience des forêts, notamment en ce qui a trait au maintien de leur régime nutritif, de leur productivité et de leur biodiversité. Les perturbations déclenchaient non seulement une dynamique de succession mais, dans certains cas, une dynamique de récurrence (cyclique) ou une dynamique régressive (état alternatif stable) (Connell et Sousa

1983, Ramade 1984, Frelich et Reich 1995). Ainsi, la forêt de pin gris sur sable, régulièrement soumise au feu, pouvait se renouveler en forêt de pin gris (récurrence) (Carleton et Maycock 1978, Cogbill 1985, Payette et al. 2012) ou encore en forêt très ouverte et en lande (Lavoie et Sirois 1998). La série évolutive de la pessière noire pouvait donc se limiter à son stade de début de succession. Dans les territoires où le feu était défavorable à la combustion de l'humus (feu de faible intensité), les forêts d'épinette noire, jadis denses et de bonne croissance, évoluaient vers des pessières noires à sphaignes et à éricacées de faible densité et même en pessières noires à lichens (Payette 1992, Payette et al. 2000, Lecomte et Bergeron 2005). Les perturbations et la dynamique forestière qu'elles instauraient et entretenaient démontraient que les écosystèmes étaient plus complexes que ce qui avait été estimé au départ (Levin et Paine 1974). Les éléments stochastiques, à l'exemple des perturbations catastrophiques, étaient également pris en compte (Chesson et Case 1986). Les relations entre le milieu physique et la végétation étaient également plus instables que sous le premier paradigme. Ainsi, dans une même entité géographique, plusieurs assemblages floristiques (végétations potentielles) pouvaient être observés sur une même combinaison de dépôts et de drainages. Par exemple, dans le domaine de la sapinière à bouleau blanc, le till mésique, surtout associé à la végétation potentielle de la sapinière à bouleau blanc, pouvait être occupé par la sapinière à épinette noire ou encore par la pessière noire (McCune et Allen 1985). Dans l'ensemble, ce concept d'équilibre dynamique des paysages rejoint ceux de la *Shifting Mosaic Steady-State* (Bormann et Likens 1979), de la *Patch dynamics* (Watt 1947, White 1979, Pickett et White 1985) et de la *Hierarchical Patch Dynamics* (Urban et al. 1987, Wu et Loucks 1995). La description présentée par Heinselman (1973) d'une portion du Minnesota (Boundary Waters Canoe Area), notamment en ce qui a trait à l'année d'origine et à la composition des forêts, est un exemple de ces concepts qui appuient l'idée que les paysages, formés de peuplements de composition et d'âges différents, évoluent selon des trajectoires dynamiques variées. Par ailleurs, certains paysages caractérisés par de grands feux et de faibles intervalles de temps entre ces feux peuvent être modifiés au point qu'un retour à la végétation initiale, ou du moins s'insérant à l'intérieur de la variabilité holocène, devient impossible (Turner et al. 1993). De tels paysages seraient alors en non-équilibre (*non equilibrium*) ou dans un état alternatif stable (Scheffer et Carpenter 2003, Jasinski et Payette 2005).

De plus, l'hétérogénéité paysagère n'est pas seulement liée à l'histoire contemporaine des écosystèmes forestiers, mais également à leur histoire plurimillénaire. En effet, l'histoire de la végétation est caractérisée par des changements de végétation synchrones avec ceux survenus dans le climat ainsi que dans le régime des feux (Payette 1992, Arseneault et Sirois 2004, Ali et al. 2012). Les cycles de feu relativement longs favorisaient les espèces de fin de succession (e.g. *Abies balsamea*) et les cycles courts, celles de début de succession (e.g. *Pinus banksiana*). La migration des espèces et des forêts vers le nord à la suite du retrait de l'Indlansis (climat chaud, peu de feux, période de l'optimum climatique 8000 – 4000 ans AA) et leur régression plus récente vers le sud (climat plus froid, feux plus fréquents, refroidissement néoglaciaire 4000 – 3000 ans AA) étaient alors déterminées par ces cycles (Payette 1993).

Enfin, à la variabilité, ou encore à la diversité inhérente aux perturbations naturelles contemporaines et plurimillénaires, s'est ajoutée celle générée par les activités anthropiques. Ces dernières étaient d'abord liées à la colonisation qui a donné lieu à de nombreux feux d'origine humaine (abattis) ainsi qu'à l'utilisation de locomotives à vapeur actionnées au charbon de bois (1850-1940). Plus tard, et sur une échelle beaucoup plus vaste, ont suivi les coupes, d'abord manuelles, puis de plus en plus mécanisées (Hardy et Séguin 1984). Ces activités ont fait en sorte que les structures d'âges des paysages ont été amputées d'une portion de plus en plus importante de vieilles forêts. La composition forestière s'est homogénéisée au profit des essences de lumière (ex. : peuplier faux-tremble), les relations entre le milieu physique et la végétation se sont obscurcies à nouveau et les limites de certaines unités écologiques ont été modifiées (Urban et al. 1987, Lorimer 2001, Grondin et Cimon 2003, Grondin et al. 2014, Laquerre et al. 2009). Les activités humaines ont fait en sorte qu'un bon nombre de paysages aménagés se situent aujourd'hui à l'extérieur de leur enveloppe de variabilité naturelle, c'est-à-dire en déséquilibre, dans une dynamique régressive ou un état alternatif stable (Bertrand 1968, Ramade 1984, Holling 1973, Connell et Sousa 1983, Chesson et Case 1986); par exemple, des paysages naturels de la zone tempérée dominés par la pruche ont été remplacés par des feuillus de lumière et ils ne sont plus dans un état d'équilibre (Rhemtulla et al. 2009).

Le paradigme de l'intégration des processus paysagers

La présente étude se situe dans la lignée des deux paradigmes précédents : le premier axé sur le déterminisme de la végétation, et le second sur un équilibre dynamique fortement lié aux perturbations naturelles. Bien que les paysages soient restés les mêmes, notre façon de les percevoir s'est modifiée à nouveau au profit d'une vision plus large et plus cohérente de l'hétérogénéité des paysages. Cette hétérogénéité est ici définie comme étant *le résultat de la complexité des interactions entre la distribution spatiale des caractéristiques environnementales et les réponses différentielles de la végétation* (White 1979, Milne 1991, Legendre 1993, Wagner et Fortin 2005). L'hétérogénéité spatiale est à la base de la définition du paysage, ce dernier étant considéré comme *une portion de territoire, de dimension variable, formée d'une mosaïque de cellules (« patches »), plus ou moins dépendantes les unes des autres, et possédant chacune des caractéristiques particulières relativement à la végétation, au milieu physique et à un ensemble de variables biotiques (ex. : perturbations naturelles et climats)* (Bertrand 1968, Daubenmire 1968, Urban et al. 1987, Robitaille et Saucier 1998, Grondin et al. 2010). L'ensemble de cette approche appartient au domaine de l'écologie du paysage qui *a comme but de comprendre l'hétérogénéité d'un territoire en le caractérisant selon la répartition géographique* *de sa végétation (pattern) et selon les causes, ou processus (process), qui provoquent une telle distribution* (Turner 1989, Turner et al. 1993, White et al. 1999). Tout considéré, le paradigme de l'intégration des processus paysagers fait partie du grand domaine de l'écologie du paysage et il se définit comme une approche intégrée de l'analyse de territoire prônant une vision holistique des variables en contrôlant le développement. Le paradigme n'est pas nouveau et il semble avoir évolué en parallèle aux deux précédents. Dès 1936, Daubenmire, dans le cadre de son doctorat, reconnaissait l'importance de l'intégration de plusieurs familles de variables (milieu physique, climat et perturbations naturelles) dans l'explication de l'hétérogénéité de son secteur d'étude au Minnesota (Big Woods). Plus récemment, Grimm (1984) réétudie le même territoire que Daubenmire (1936) et montre l'influence majeure des activités anthropiques. Les travaux du pédologue américain Jenny (1958), popularisés au Québec par Jurdant et al. (1977), jouent un rôle de premier plan dans la reconnaissance du paradigme de l'intégration. Le paradigme englobe les concepts et les analyses associés aux gradients écologiques et à leur expression sur les ordinations (Whittaker 1967, Økland 1996). Peu à peu, le concept de l'hétérogénéité des paysages s'est en quelque sorte rapproché de celui portant sur une meilleure caractérisation des structures spatiales (Legendre et Fortin 1989, Legendre 1993). En d'autres termes, comprendre l'hétérogénéité des paysages est sensiblement la même chose qu'en définir les structures spatiales. La reconnaissance du paradigme de l'intégration comme étant au centre de la compréhension de la structure spatiale définissant l'hétérogénéité des paysages ne doit pas être perçue comme allant à l'encontre de la théorie neutre proposée par Hubbell (2001). Cette dernière accorde priorité à une répartition des espèces contrôlée par un ensemble de processus biotiques, telles que la croissance, la reproduction, la mortalité et la migration. Nous estimons que la compréhension de l'hétérogénéité des paysages doit prendre en compte les deux grandes théories parce que toutes les deux sont explicatives de la diversité des paysages (Gravel et al. 2006). Des auteurs contemporains ont démontré et quantifié le chevauchement de la végétation et de ses variables explicatives le long des gradients écologiques par le biais de l'écologie numérique, notamment en utilisant le partitionnement de la variation de la végétation (Borcard et al. 1992, Legendre 1993, Tuomisto et al. 2003, Legendre et al. 2005, Dray et al. 2012). Toutefois, l'inclusion systématique de ces quatre familles de variables, comprenant en particulier les perturbations naturelles et humaines dans l'ensemble des facteurs de structuration des paysages boréaux, et l'étude de leur complémentarité, est une démarche qui n'avait pas encore été entreprise, et c'est là l'originalité de notre étude.

Objectifs et structure de la thèse

Dans un contexte d'aménagement écosystémique efficace, il est important de comprendre les processus qui façonnent l'hétérogénéité des paysages forestiers. Explorer le contenu de cette hétérogénéité selon une vision intégratrice de plusieurs familles de variables explicatives est ainsi au cœur de notre réflexion. Trois aspects seront abordés :

1- les gradients écologiques, les structures spatiales (cartes) et l'estimation de l'importance des variables environnementales dans la variation de la végétation décrite selon trois thèmes (espèces forestières, types forestiers, végétations potentielles-stade évolutifs),

2- l'expression dans l'espace des liens entre la végétation et ses variables explicatives, telle que définie par des entités géographiques relativement similaires, au regard de la végétation et de leurs variables explicatives (unités homogènes de végétation), 3- et la comparaison de paysages formés par les processus naturels avec les paysages aménagés formés des mêmes processus, mais auxquels s'ajoutent les activités anthropiques.

Le premier chapitre s'intéresse aux facteurs (familles de variables explicatives, *drivers*) régissant l'hétérogénéité des paysages. Nous avons abordé cette problématique dans l'objectif de vérifier l'influence sur l'hétérogénéité de la végétation à l'échelle du paysage de trois thèmes de végétation : les espèces forestières, les types forestiers et les combinaisons de la végétation potentielle et des stades évolutifs. Premièrement, nous avons posé l'idée de liens étroits 1) entre les espèces forestières et le climat, 2) entre les végétations potentielles-stades évolutifs et les perturbations naturelles 3) ainsi qu'entre les types forestiers et le milieu physique. Deuxièmement, nous avons voulu vérifier si, malgré la spécificité des thèmes de végétation, l'hétérogénéité de la végétation des paysages demeure principalement expliquée par l'intégration de plusieurs familles de variables explicatives. Enfin, nous avons tenté d'évaluer l'effet des perturbations anthropiques, présentes sur le territoire depuis environ un siècle, par rapport aux autres familles de variables explicatives considérées comme naturelles.

Le second chapitre, qui s'inscrit dans le domaine de la classification écologique du territoire (*Ecological land classification*), vise à analyser l'hétérogénéité du territoire d'étude pour y délimiter des espaces (paysages relativement homogènes) en se basant sur la végétation et sur quatre familles de variables explicatives (climat, environnement physique, perturbations naturelles et perturbations humaines). La classification des paysages selon un système hiérarchique a été établie en segmentant les gradients écologiques caractérisant le territoire en entités géographiques de dimensions de plus en plus restreintes et aux caractéristiques de plus en plus similaires. Les entités ainsi définies ont été dénommées *unités homogènes de végétation*. Le terme *unité homogène* permet d'opposer les concepts d'hétérogénéité et d'homogénéité (McIntosh 1991) car, bien que le territoire d'étude soit hétérogène, la présence et l'analyse de gradients écologiques formés par le chevauchement de variables descriptives et explicatives mènent à la délimitation de portions de territoire de plus en plus homogènes formant une hiérarchie (Dufrêne et Legendre 1991, Dufrêne 1992, Gerardin et Ducruc 1990). Alors que dans le premier chapitre nous avions utilisé le partitionnement de la variation de la végétation afin de distinguer les thèmes de végétation, dans celui-ci, le partitionnement est utilisé afin d'estimer la contribution des familles de variables explicatives aux divers niveaux de perception d'unités homogènes.

Le troisième chapitre, tout en s'inscrivant dans la poursuite des deux précédents, se situe davantage dans la démarche d'élaboration et de mise en œuvre de l'aménagement écosystémique et vise à comparer les paysages naturels et les paysages aménagés selon leur structure d'âge et leur composition. *Le paysage naturel est celui qui évolue sous l'effet des processus écologiques contemporains et plurimillénaires, sans intervention anthropique* (Grondin et al. 2010). Le paysage naturel des unités homogènes (n=14) a été qualifié d'une variabilité naturelle contemporaine et plurimillénaire, sur la base d'études spécifiques au cycle des feux (Bergeron et Dansereau, 1993, Leduc et al. 1995, Gauthier et al. 1996, Carcaillet et al. 2010). Chaque paysage naturel a ensuite été comparé au paysage actuel, c'est-à-dire celui observé de nos jours, puis chacun de ces couples a été qualifié relativement à son état d'équilibre et à sa résilience. Le paysage naturel défini pour chacune des unités homogènes est considéré comme l'état de référence pour l'aménagement écosystémique.

En conclusion, les divers chapitres de l'étude s'enchaînent les uns aux autres en tendant vers une vision de plus en plus fine de l'hétérogénéité des paysages résultant de l'action intégrée de la végétation et de ses variables explicatives (process). Une fois cette hétérogénéité comprise et définie le long de gradients écologiques, il devient dès lors possible de segmenter le territoire en portions relativement homogènes (patterns). Ces unités sont utilisées afin de comparer les paysages naturels et les paysages aménagés. Dans l'ensemble de la démarche, les connaissances sur les variables explicatives s'accumulent et permettent de constater que, même si l'influence des perturbations naturelles et humaines y occupe une place de choix, l'intégration demeure le processus dominant.

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CHAPITRE I

DRIVERS OF CONTEMPORARY LANDSCAPE VEGETATION HETEROGENEITY IN THE CANADIAN BOREAL FOREST: INTEGRATING DISTURBANCES (NATURAL AND HUMAN), CLIMATE AND PHYSICAL ENVIRONMENT

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En voie de publication dans la revue *Ecoscience*

1.1 Résumé

Cette étude vise à démontrer que l'hétérogénéité des paysages contemporains est contrôlée par les perturbations naturelles en combinaison avec d'autres familles de variables explicatives. L'intégration de ces facteurs (drivers) devrait être considérée comme l'élément clé permettant d'expliquer les changements de la végétation survenant le long des gradients écologiques qui caractérisent la forêt boréale. Des placettes d'inventaire forestier et des cartes forestières produites de 1970 à 2000 ont été utilisées pour caractériser un vaste territoire (175 000 km^2) selon trois thèmes de végétation (espèces forestières, types forestiers, végétations potentielles-stades évolutifs) et quatre familles de variables explicatives (climat, perturbations naturelles, milieu physique et perturbations humaines). Des ordinations canoniques ont été effectuées pour définir les gradients écologiques et, le long de chacun d'eux, caractériser le chevauchement entre les thèmes de la végétation et les familles de variables explicatives. Pour chaque thème, on a quantifié la proportion relative de la variation de la végétation expliquée par les familles seules (aucun chevauchement) ou en combinaison avec les autres. L'hétérogénéité de la végétation décrite par les espèces ainsi que par les végétations potentielles-stades évolutifs s'explique principalement par les perturbations naturelles et le climat en association avec d'autres familles de variables explicatives. L'hétérogénéité de la végétation décrite par les types forestiers est encore dominée par les perturbations naturelles et le climat, mais le milieu physique est plus important que dans les deux autres thèmes. Par rapport aux familles naturelles de variables explicatives, les perturbations humaines jouent un rôle secondaire mais significatif dans les trois thèmes de végétation.

L'ensemble de cette information sur les relations entre la végétation et les facteurs à la base de son développement contribue à une meilleure connaissance du territoire d'étude et constitue un pas de plus vers son aménagement écosystémique.

Mots-clés : gradients écologiques, hétérogénéité paysagère, intégration de familles de variables explicatives, partitionnement de la variation

1.2 Abstract

This study aims to demonstrate that contemporary landscape vegetation heterogeneity is controlled by a combination of natural disturbances with other sets of explanatory variables. The integration of these drivers should be considered as the key to explaining vegetation changes along ecological gradients characterizing the boreal forest. Forest inventory plots and maps produced from ≈1970 to 2000 were used to characterize a large area (175 000 km^2) according to three vegetation themes constituting distinct aspects of forest community composition (tree species, forest types, and potential vegetation–successional stages) and four sets of explanatory variables (climate, natural disturbances, physical environment and human disturbances). Canonical ordinations were performed to define ecological gradients as well as the overlap between vegetation themes and sets of explanatory variables along each gradient. For each vegetation theme, we quantified the relative proportion of vegetation variation explained by unique as well as combined sets of explanatory variables. The landscape vegetation heterogeneity described by species and potential vegetation-successional stage is mostly explained by natural disturbances and climate in association with other sets of explanatory variables. Landscape vegetation heterogeneity related to forest types is still dominated by natural disturbances and climate, but the influence of the physical environment is higher than for the other themes. Compared to natural sets of explanatory variables, human disturbances play a secondary but significant role in the three vegetation themes. This information about the relationship between vegetation and the factors underlying its development contributes to a better understanding of the boreal forest and represents an important step forward toward ecosystem-based management.

Keywords: ecological gradients, integration of sets of factors, landscape heterogeneity, variation partitioning.

Nomenclature: Scoggan (1978)

1.3 Introduction

Ecosystems are spatially heterogeneous because of the diversity created by vegetation and environmental characteristics (White, 1979; Wagner & Fortin, 2005; Milne, 1991). This heterogeneity characterizes the landscape, defined as an area fragmented into a mosaic of interconnected patches, each showing particular characteristics in terms of vegetation, abiotic variables (e.g., physical environment), biotic factors (e.g., species competition), and processes (natural and anthropogenic) (Daubenmire, 1968; Urban *et al.*, 1987; Perera & Euler, 2000). In this study, we defined landscape heterogeneity (diversity) on the basis of ecological gradients and evaluated the relative contribution of factors controlling this diversity, which are important concerns in landscape ecology (Turner, 1989; White *et al.*, 1999; Wu & Loucks, 1995).

As a first step toward defining the landscape heterogeneity of the study area, we used three vegetation themes (response variables) representing three distinct aspects of forest composition. The first theme describes tree species and their abundance. At this level, the distribution of vegetation is the result of migration, dispersal processes, interspecies competition, species autecology, and environmental factors (climate, physical environment, disturbances) along the ecological gradients of latitude, longitude, and altitude (Gleason, 1939; Whittaker, 1967; Ohmann & Spies, 1998; Hubbell 2001). The second theme consists of forest types, namely, groups of tree species with similar ecological affinities. Each forest type has its own set of ecological preferences (ecological niches), having established at locations with appropriate living conditions (Whittaker, 1967; Hutchinson 1957; Damman, 1964; Gauvin & Bouchard, 1983; Legendre *et al.*, 2005). The third theme is made up of potential vegetations, defined as specific assemblages of tree species that are linked by the dynamics of their successional stages (Dansereau, 1957; Rey, 1960; Daubenmire, 1968; Powell, 2000; Saucier *et al.*, 2009; Cyr *et al.*, 2012). For example, in Quebec's boreal forest, *Betula papyrifera*, *Populus tremuloides*, *Abies balsamea*, and *Picea glauca* constitute an assemblage observed on sites with specific combinations of physical features, microclimate and disturbances. The early-successional stage is dominated by light-demanding species (e.g., *Betula papyrifera*); with increasing time since the last fire, they are progressively replaced by the shade-tolerant species that compose the late-successional stage (e.g., *Abies balsamea*) (Bergeron, 2000; Couillard *et al.*, 2012).

As a second step toward defining the landscape heterogeneity of the study area, we used four sets of explanatory variables (factors): climate, natural disturbances, physical environment and human disturbances. It is well known that, at a continental scale (biomes), patterns of vegetation are associated with large-scale climatic variations (Hare, 1950; Whittaker, 1960; Damman, 1979; Bailey, 1987; Ohmann & Spies, 1998). The climate-fire connection is a key process affecting contemporary and Holocene boreal vegetation diversity, dynamics, and resilience (Heinselman 1973; Payette, 1992). Major differences in vegetation can be observed between maritime areas and the continent's interior, due to specific climate-fire relationships (fire-cycle and species responses) (Ohmann & Spies, 1998; Parisien & Sirois, 2003; Cyr *et al.*, 2007; Bouchard *et al.*, 2008). The effects of natural disturbances, mostly fires, are influenced by the physical environment. Landscape configuration, including topography and abundance of wetlands and water bodies, is a major determinant of fire behavior and landscape heterogeneity (Whittaker, 1960; Rowe & Scotter, 1973; Zackrisson, 1977; Peet, 1978; Romme & Knight, 1981). The relationship between climate and physical environment (elevation, altitude) becomes a dominant factor in regions where stand-replacing disturbances are relatively rare (long fire cycle), as in the mountainous wet maritime landscapes of northwestern North America (Whittaker, 1960; Reiners & Lang, 1979; Swanson *et al.*, 1988; Turner & Romme, 1994; Ohmann & Spies, 1998; Lertzman & Fall, 1998). Landscape vegetation heterogeneity is also influenced by human disturbances. The combined action of naturally-occurring fires, human-caused fires, and logging has a major impact, increasing the proportion of early-successional species and the loss of old-growth forests (Grimm, 1984; White & Mladenoff, 1994; Foster *et al.*, 1998; Cushman and Wallin, 2002; Grondin & Cimon, 2003; Ohmann *et al.*, 2007; Boucher *et al.*, 2009). Our study area has been subjected to human activities, particularly forest harvesting and fires in the southern part, for almost 150 years.

A holistic approach to explaining landscape heterogeneity, based on the integration of several sets of variables (climate, physical environment, natural disturbances, and human disturbances), has evolved since the early 20th century (Daubenmire, 1936; Jenny, 1958; White, 1979; Turner, 1989). Daubenmire (1936) demonstrated, in the relatively natural Big Woods area (Minnesota, USA), that the spatial transition from prairie to woodland to forest ecosystems was related to the combination of climate, natural disturbances, and physical environment. In the same area, Grimm (1983, 1984) showed that, over the past decades, landscapes had been strongly modified by human activities, which are now considered to be the main factor controlling landscape dynamics.

However, these approaches, although holistic in their conception, did not take into account all of these themes and factors at the same time. Here, we quantified the relative contribution of four sets of explanatory variables, including recent anthropogenic influences, to the landscape heterogeneity of a vast territory described according to three vegetation themes. Although Quebec has a rich history of ecological land classification (Jurdant *et al.*, 1977; Grondin *et al.*, 2007; Saucier *et al.*, 2009), quantitative estimates of the natural and human drivers that modulated its landscape heterogeneity are still in the embryonic stage. This study aims first to demonstrate that the proportion of the vegetation heterogeneity explained by various sets of explanatory variables (factors) differs according to the three vegetation themes. More specifically, we expect the strongest links to be 1) between the tree species theme and climate, 2) between the forest types theme and physical environment and 3) between the potential vegetation-successional stages theme and natural disturbances. Second, we will show that despite the specificity of themes, landscape vegetation heterogeneity is mainly related to the integration of natural disturbances with other sets of explanatory variables. Finally, we will establish that human disturbances are a secondary, yet important cause of landscape heterogeneity, despite their relatively recent appearance in the study area (~150 years).

1.4 Methods

1.4.1 Study area

The 175 000-km^2 study area forms part of Quebec's boreal forest, more precisely, the *Abies balsamea–Betula papyrifera* domain in the south and the *Picea mariana*–feathermoss domain in the north (Saucier *et al.*, 2009, Figure 1.1, study area center at 49° 15' N and 75° 35' W). This area is appropriate for the objectives of our study because of its very diverse natural and human forest landscapes and large size (Robitaille & Saucier, 1998; Grondin *et al.*, 2007; Saucier *et al.*, 2009). The forest vegetation consists mainly of six tree species: *Picea mariana* (Mill.) B.S.P., *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss, *Pinus banksiana* Lamb., *Betula papyrifera* Marsh., and *Populus tremuloides* Mich.

The average annual temperature varies from 1.5°C in the south to -1.5°C in the north. During the growing season (May to September), precipitation (rainfall) ranges from about 300 mm in the Abitibi region (west) to 350 mm in the Lac-Saint-Jean region (east), following a longitudinal gradient. Abitibi is characterized by organic and glaciolacustrine deposits as well as a relatively flat topography, while till, glaciofluvial deposits, and a relatively hilly topography are found in the Lac-Saint-Jean region (Robitaille & Saucier, 1998; Grondin *et al.*, 2007). Fires and spruce budworm outbreaks have been the main natural disturbances throughout the study area. Fires occurred over huge areas in the 1820s-1870s and 1920s (Bergeron *et al.*, 2001; Lesieur *et al.*, 2002; Grondin *et al.*, 2007). Three spruce budworm outbreaks, peaking around 1910, 1950, and 1975-1980, affected the age structure and composition of vegetation in the 20th century (Morin, 1994; Bergeron *et al.*, 2001).

From 1870 to 1950, forest harvesting and land clearing were carried out in both the Abitibi and Lac-Saint-Jean regions, particularly along a railway line built between 1905 and 1910 that runs across the southern part of the territory. The line's early coal-powered steam locomotives contributed to human-caused forest fires in subsequent decades (Hardy & Seguin, 1984; Grondin & Cimon, 2003; Laquerre *et al.*, 2009). During the second half of the 20th century, mechanized logging spread throughout the southern part of the study area (*Abies balsamea–Betula papyrifera* domain) and, gradually, towards the northern part (*Picea mariana*–feathermoss domain).

1.4.2 Data sources and matrices

This study is based on forest maps and forest inventory plots produced between the 1970s and 2000 by the Ministère des Ressources naturelles du Québec (MRN) (Letarte *et al.*, 1995). These data were used to develop matrices describing 606 landscape units refered to as ecological districts (Figure 1.2A1). Each of the ecological districts (mean area of 200 km^2) is relatively homogeneous in terms of surficial deposits, topography, geology, and regional vegetation (Robitaille & Saucier, 1998). Each was described with regard to two matrices: vegetation (Y-matrix of response variables) and factors (X-matrix of explanatory variables) (Figure 1.2A2). The rows of the two matrices represent the ecological districts, and the columns, the response or explanatory variables.

The Y-matrix contains three vegetation themes: tree species composition (botanical aspect, m=10), forest types (site aspect, m=14), and potential vegetation-successional stages (forest dynamics aspect, m=12) for a total of 36 variables (Appendix 1). The first theme describes the relative proportion of 10 tree species in each ecological district based on forest inventory plots (n = 53 635). The second theme describes the relative proportion of 14 forest types in each ecological district based on forest maps. The third theme describes the vegetation with respect to the potential vegetation types (n=3) and successional stages (n=4) associated to each forest inventory plot. Three types of potential vegetation were considered: *Abies balsamea-Betula papyrifera* (Ms2), *Abies balsamea-Picea mariana* (Rs2), and *Picea mariana* (Re2).

The X-matrix contains four sets of explanatory variables: climate (m = 8), natural disturbances (m = 12), physical environment (m = 16), and human disturbances (m = 8), for a total of 44 variables (Appendix 2). The climate (C) of each of the 606 ecological districts was characterized using the BioSIM simulator designed by the Canadian Forest Service (Régnière, 1996). The climatic variables were estimated for the center of each ecological district using data from 37 meteorological stations located in the study area. Natural disturbances (ND) were described relative to the history of fires and spruce budworm outbreaks over the last 150 years. Forest maps were used to describe the relative proportion of each ecological district affected by light or severe insect outbreaks and natural fires. Forest inventory plots provided information according to the time since the last fire and type of disturbance (spruce budworm outbreaks). Post-fire forest types (1851f, 1891f, 1921f) formed distinct categories from post-spruce budworm outbreak forest types (1851o, 1891o, 1921o). Physical environment (PE) was described using a MRN database containing the relative proportion of surficial deposits and physiographic variables (e.g., mean altitude) for each ecological district (Robitaille & Saucier, 1998). Human disturbances (HD) were analyzed based on forest maps, forest inventory plots, and archival data on human disturbances (MRN). The history of contemporary human activities has been presented in Grondin *et al.* (2014).

1.4.3 Data analysis

The 2 databases (Y- and X-matrices) were analyzed in order to describe the ecological gradients linked to geographical units defined for each vegetation theme and set of explanatory variables. A comparison of the geographical units located on, first, the vegetation theme ordination (Figure 1.4A) and, second, the explanatory variable ordination (Figure 1.4B) revealed some overlap, the degree of which was quantified using variation partitioning of the vegetation.

1.4.3.1 Ecological gradients

Multivariate analyses such as redundancy analysis are invaluable tools for studying landscape heterogeneity (Legendre et Legendre 2012). The two matrices (Y- response variables and X- explanatory variables) were analyzed in order to describe and associate ecological gradients characterizing the vegetation and explanatory variables (Whittaker, 1960, 1967; Peet, 1978, Figure 1.2, Appendices 1,2). Comparison of the ordination of response variables and the ordination of explanatory variables allowed us to understand the overlap between the two sources of information (Appendix 3). Variation partitioning then provided the statistical means to quantify the relative contribution of different sets of explanatory variables to vegetation heterogeneity (Borcard *et al.*, 1992; Ohmann & Spies, 1998; Legendre *et al.*, 2005; Dray *et al.*, 2012).

To model ecological gradients, a redundancy analysis (RDA) was performed on the Y- and X-matrices (Figure 1.2A2) (Borcard *et al.*, 2011; Legendre & Legendre, 2012; Dray *et al.*, 2012) using the vegan package (Oksanen *et al.*, 2010) of the R statistical language (R Development Core Team, 2010). The objective of an RDA is to extract the variation of a set of response variables (Y-matrix) explained by a set of explanatory variables (X-matrix). In an RDA, we perform a regression analysis (first step) of all explanatory variables on each response variable, and then produce a matrix of fitted values, which is then subjected to a principal component analysis (PCA; second step). The RDA results in an ordination diagram that summarises, by canonical axes, the spatial patterns and heterogeneity of the Y matrix that is explained by the X matrix.

Considering the large number of response (36) and explanatory variables (44), it was useful to group them in order to provide a summary of the information. RDA and *k*-means clustering were conducted using vegan (Figure 1.2A3). *K*-means clustering was carried out on all canonical axes of the RDA in order to group the variables belonging to the vegetation themes (9 groups were retained) as well as the variables composing the sets of explanatory variables (11 groups were retained) (Figure 1.2A4). Each group was named and described using the most representative variable for the group. The groups of response variables and the groups of explanatory variables are presented on distinct ordinations (Figure 1.2A5).

The principle of variation partitioning consists in a series of partial linear regressions or RDA (Borcard *et al.*, 1992; Legendre *et al.*, 2005; Legendre et Legendre 2012; Peres-Neto *et al.*, 2006). Each partial RDA consists in an analysis of the response variables Y on explanatory variables X in the presence of additional explanatory variables, called covariables. In partial RDA, the linear effects of explanatory variables X on response variables Y are adjusted for the effects of the covariables. To complete the Venn diagram consisting of four sets of explanatory variables (Figure 1.2B), 16 partial RDAs are required, and the result of each one is an adjusted R^2 of the variation explained by a unique set or by a combination of two, three or four sets of explanatory variables. Variation partitioning was computed using the varpart function of the vegan package, following the steps proposed by Borcard *et al.* (2011) (Appendix 4).

1.5 Results

The results consist first of a description of the ecological gradients used to characterize the study area in terms of vegetation (first ordination) and explanatory variables (second ordination). This description allows us to understand the organization (landscape heterogeneity) of the study area along with the overlap between the response and explanatory variables. Once the area has been presented, variation partitioning (second section) is used in order to achive the three aims of the study. Thus, the ecological gradients are a prerequisite to understanding the variation partitioning.

1.5.1 Ecological gradients

Groups of response variables and explanatory variables were considered in terms of geographical distribution (maps), position on the ordination diagrams, and gradual changes along ecological gradients. For clarity, the groups are illustrated on two separate ordination diagrams. Axes 1 (vertical) and 2 (horizontal) reflect the geographic organization of the territory. Each of the nine groups of vegetation variables is composed of variables belonging to the three vegetation themes (Figures 1.3A, 1.3B, Table 1.1, Appendix 1). Each of the 11 groups of explanatory variables is made up of variables belonging to the four sets of explanatory variables (Figures 1.3C, 1.3D, Table 1.1, Appendix 2).

Table 1.1 Codes used to describe groups (prefix G) of vegetation variables and groups of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]). Each group is composed of some variables presented in Appendices 1 and 2.

The first three canonical axes of the RDA explain 33% of vegetation heterogeneity. On both ordination diagrams (Figures 1.3B, 1.3C), axis 1 describes the changes along the latitudinal gradients, i.e., the gradual transition from the *Abies balsamea-Betula papyrifera* bioclimatic domain (south) to the *Picea mariana*-feathermoss domain (north). The vegetation characterizing the southern part of the latitudinal gradient is dominated by the *Betula papyrifera* forest type (GBepaF) and *Abies balsamea* species (GAbbaS) (Figures 1.3A, 1.3B). In the more northern landscapes, these groups gradually give way to the *Picea mariana* forest type (GPimaF) and wetlands groups (GWetlands). The southern landscapes include some temperate zone tree species, grouped under GAcruS, including *Acer rubrum* L., *Betula alleghaniensis* Britt., and *Thuja occidentalis* L. The study area is also characterized by a southeast to northwest latitudinal-oblique gradient, which shows a gradual transition from the *Picea mariana-Abies balsamea* forest type (GPimaAbbaF, southeast) to non-forested wetlands (GWetland, northwest). Along the latitudinal gradient, the explanatory variables (Figures 1.3C, 1.3D) first show a decrease in the annual number of growing degree-days (GGdd) in both areas affected by light spruce budworm outbreaks (GSbom) and in those characterized by significant logging (GLog1). Second, they show an increase in fires during the 1851 period (G1851f). The latitudinal-oblique gradient describes the gradual transition from southeastern hilly landscapes (high GEle values) to flatter northwestern landscapes dominated by organic soils (GD_7).

Axis 2 describes the changes along the longitudinal gradient. The vectors associated with this axis are short, indicating that they have less influence on the distribution of the vegetation than axis 1. For vegetation themes (Figure 1.3B), the western (left) portion of the diagram is mainly occupied by the *Populus tremuloides* (GPotrF), *Populus tremuloides-Picea mariana* (GPotrPimaF), and *Pinus banksiana* (GPibaF) forest types. The explanatory variables (Figure 1.3C) defining the longitudinal gradient are: 1) relatively high atmospheric aridity (GAri) and a high frequency of human-induced fires (GHfl) in the southwest, 2) glaciolacustrine clay surficial deposits (GD_4ga) and fires during the 1921 period (G1921f) characterizing the western central area, and 3) fires during the 1891 period (G1891f) in the central part (slightly west) of the study area.

Comparing a position on the ordination of the groups of response variables (Figure 1.3B) with the same position on the ordination of the groups of explanatory variables (Figure 1.3C) allows us to confirm the overlap of these groups. For example, on the ordination of response variables, the *Abies balsamea* group (GAbbaS, Figure 1.3B) occupies the same position occupied by the spruce budworm outbreaks group on the ordination of explanatory variables (GSbom, Figure 1.3C). The two groups thus overlap in the same location: the southern and south-eastern parts of the study area (Appendix 3).

1.5.2 *Variation partitioning*

Variation partitioning shows that the total variation of the vegetation explained by the explanatory variables is relatively high and increases from the potential vegetation-successional stages theme (55%) to the tree species theme (58%) and again to the forest types theme (69%) (Table 1.2, upper part). The total relative proportion of explained variation associated with natural disturbances (NDt) is high for the potential vegetation-successional stages (89%) and tree species (78%) themes. This variation (NDt) is lower for the forest types (67%), but still remains the most important set. The variation associated to unique fractions is generally low, except for natural disturbances (NDu) in the tree species theme (25%) and the potential vegetation-successional stage theme (37%) (Figure 1.4, Table 1.2). These two fractions represent the highest of the 15 fractions composing the variation partitioning. The total variation explained by common fractions (e.g., NDc) is always much higher than the total variation explained by unique fractions (e.g., NDu). For the tree species and potential vegetation-successional stage themes, the common fractions of vegetation variation (double, triple, and quadruple combinations) decrease from natural disturbances (NDc) to climate (Cc), physical environment (PEc), and human disturbances (HDc). For the forest types theme, the common fractions related to NDc (55%), PEc (49%), and Cc (47%) are high and relatively similar (Figure 1.4, Table 1.2). These results demonstrate the strong influence of natural disturbances on vegetation variation.

In the forest types theme, the variation described by natural disturbances (NDt, 67%) is still high, but similar to that of the physical environment (PEt, 62%) (Table 1.2). Values of R^2_{adj} for vegetation themes and each natural set of explanatory variables (PE, C, ND) are similar for the tree species and potential vegetation-successional stages themes; they are higher for the physical environment (43%) and climate (36%) under the forest type theme (Table 1.3). These results demonstrate that the three vegetation themes are different in regard to their variation partitioning.

Among the double combinations of natural sets of explanatory variables (i.e., those which do not involve human disturbances), the PE∩ND combination explains the largest fraction of vegetation variation, while the double combinations including climate (PE∩C, C∩ND) explain smaller fractions (Table 1.2, lower section). The triple combination of natural sets (PE∩C∩ND) explains the largest fraction of variation. These results show the relatively high proportion of vegetation variation explained by the combinations of natural sets of explanatory variables.

Table 1.2 Detailed view of the relative proportion of vegetation variation (%) explained by four sets of explanatory variables (climate [C], natural disturbances

[ND], physical environment [PE], and human disturbances [HD]) in relation to three vegetation themes. Partial canonical analysis (Y- and X-matrices) estimates the total explained and unexplained variation. The explained variation is divided into 15 fractions (Figure 1.2B). The unique fractions (e.g., PEu) are associated with only one set of explanatory variables, while the common fractions (e.g., PE∩C) are associated with more than one set. The common relative variation by a set is the sum of double, triple, and quadruple fractions containing this set (e.g., PEc = [PE∩C]+[PE∩HD]+[PE∩ND]+[PE∩C∩ND]+[PE∩HD∩C]+[PE∩HD∩ND]+ [PE∩HD∩ND∩C] - 7 fractions). The total relative variation by a set is the sum of unique and common fractions (e.g., [PEt]=[PEu]+[PEc] - 8 fractions). See also Figure 1.4 for a synthetic presentation of the results.

Table 1.3 R^2_{adj} for each vegetation theme in relation to four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]).

Human disturbances explain smaller fractions of total and common relative variation (approximately 30% for HDt and 25% for HDc) than natural sets of explanatory variables; they also show low values of R^2_{adj} for all vegetation themes (Table 1.3). Some combinations including HD and ND are significant and reflect the overlap of these two sets. The triple combination of HD∩ND∩C is larger than any double (PE∩HD, C∩HD, and HD∩ND) or triple combination that includes human disturbances (PE∩HD∩C and PE∩HD∩ND). However, the sum of all fractions containing the HD∩ND combination remains lower than the sum of all fractions including the PE∩ND combination (Table 1.2, lower section). These results show that human disturbances are a secondary, yet important cause of landscape heterogeneity, despite their relatively recent appearance in the study area.

1.6 Discussion

Previous studies that defined ecological gradients of a territory and quantified the contribution of several sets of explanatory variables to landscape vegetation heterogeneity were mainly conducted in areas characterized by a strong altitudinal gradient (Whittaker, 1967; Romme & Knight, 1981; Ohmann & Spies, 1998; Cushman & Wallin, 2002). In our study area, gradients are more numerous and are characterized by various directions: from south to north (latitudinal gradient), west to east (longitudinal gradient), and southeast to northwest (latitudinal-oblique gradient). There is a synchronicity between changes in vegetation and changes in sets of explanatory variables (climate, natural disturbances, physical environment, human disturbances) along all of these gradients, as revealed by the high proportion of the total vegetation variation explained primarily by the combinations of these sets. The landscape heterogeneity is therefore structured (organized), because the spatial pattern of the forest mosaic reflects the relationship between vegetation and environmental characteristics (Wagner & Fortin, 2005; Legendre *et al.*, 2005; Legendre et Legendre 2012; Dray *et al.*, 2012). All parts of the forest mosaic are not equivalent. Landscapes are composed of different types of habitats and each has its own ecological processes. Structured heterogeneity has been observed regardless of the theme used to describe the vegetation. Hubbell's (2001- neutral theory) and Hutchinson's (1957-niche theory) concepts are more similar than one might expect (Gravel *et al.*, 2006- continuum hypothesis) Therefore, toposequences showing the spatial organization (vegetation and explanatory variables) of a territory are relevant (Blouin & Berger, 2005). In the study area, ecological gradients vary according to vegetation themes, which determine the framework of the discussion.

1.6.1 *Heterogeneity of tree species and potential vegetation-successional stages: the latitudinal gradient*

The characterization (organization, structuration) of landscape heterogeneity is similar for these two themes. Their ecological gradients and variation partitioning are closely related. The latitudinal gradient is dominant (Figures 1.3 and 1.5) and natural disturbances explain the largest fractions of vegetation variation (Figure 1.4). Specificity of tree species in relation to latitudinal gradient is well-known (e.g., Damman, 1979; Ohmann & Spies, 1998). Specificity of potential vegetation-successional stages in regards to a latitudinal gradient has been noted in works concerning ecological classification (e.g., Powell, 2000; Saucier *et al.*, 2009). In the study area, the abundance of the three types of potential vegetation (*Abies balsamea-Betula papyrifera* (Ms2), *Abies balsamea-Picea mariana* (Rs2), and *Picea mariana* (Re2)) shows a decrease from the south towards the north (Grondin *et al.*, 2014).

Three elements explain the high proportion of variation assigned to natural disturbances regarding the themes of tree species and potential vegetation-successional stages. First, natural disturbances are characterized by substantial unique variation, mainly caused by large portions of the study area having been affected by a uniform abundance of insect outbreaks or fires. For example, the central portion of the study area has numerous stands originating from the 1921 fire period. The areas affected by these landscape-scale processes are more uniformly distributed than those affected by gradual changes caused by other sets of explanatory variables, for example a relief varying from hilly to undulated or flat along a specific ecological gradient (Appendix 3E). The high unique variation of the natural disturbance set reveals the relative independence of this set from changes in vegetation and other sets of explanatory variables. The finding that natural disturbances are the major driver of landscape heterogeneity, without necessarily having links with other sets, concurs with many other studies (Heinselman, 1973; Payette, 1992; Ali *et al.*, 2008; de Lafontaine & Payette, 2011).

Second, natural disturbances overlap other natural sets to a large extent. For all vegetation themes, the fractions of variation associated to combinations involving natural disturbances (especially combined with physical environment or with physical environment and climate) are much higher than the fraction associated to natural disturbances as the unique source of variation. These results concur with those of several authors who emphasized natural disturbances and physical environment in explaining intra-regional heterogeneity. When larger territories are considered, climate is inserted into the most important combination of explanatory variables (e.g., Peet, 1978). The predominance of combinations of natural disturbances with climate (e.g., Ohmann & Spies, 1998; Parisien & Sirois, 2003; Bouchard *et al.*, 2008) and physical environment (e.g., Rowe & Scotter, 1973; Zackrisson, 1977; Peet, 1978; Hemstrom & Franklin, 1982) is the basis of the integrated concept promoted in this study (second hypothesis).

Third, a proportion of variation explained by natural disturbances is attributable to the combination of this set with human disturbances. Although the fraction of landscape vegetation heterogeneity explained by human disturbances (HDt) is smaller than that of natural sets of explanatory variables (Ct, NDt, PEt), two combinations involving natural and human disturbances explain a relatively high proportion of variation ($HD \cap ND$, $HD \cap ND \cap C$). Variation partitioning clearly demonstrates that human disturbances are a secondary, yet important cause of landscape heterogeneity, despite their relatively recent appearance in the landscape (third hypothesis). Over time, the combination of human disturbances with natural sets of explanatory variables could become more important than the combination of natural sets alone, as is the case in Europe (e.g., Bradshaw & Hannon, 1992) and in the Canadian temperate forest (e.g., Boucher *et al.*, 2009). At that point, the study area would be more strongly affected by human disturbances, and perhaps, climatic conditions (Périé *et al.*, 2014).

1.6.2 *Heterogeneity of forest types: the latitudinal-oblique gradient*

The landscape heterogeneity of the forest types theme is mainly associated with the latitudinal-oblique gradient. Natural disturbances and climate are also the most important sets of explanatory variables, but the role of physical environment is more significant than in other themes. This phenomenon is illustrated in Figure 1.5, where the distribution of *Abies balsamea* as a forest type is closely related to that of physical environment, particularly elevation (GEle, Figure 1.3). Specificity of forest types according to their site characteristics has been reported in numerous phyto-sociological studies (e.g., Damman, 1964; Gauvin & Bouchard, 1983). This interpretation is close to the Hutchinsonian view of ecosystems and niche control of the spatial distribution of the vegetation. The unique fraction associated to natural disturbances is relatively small here. This indicates that, for this theme, the changes in natural disturbances along ecological gradients are mostly synchronous with those of other sets.

The vegetation variation explained by the unique fraction of the physical environment is generally small, except in the forest types theme, where it is moderate. This indicates that the same physical environment may be affected by a variety of processes related to natural disturbances. For example, thick till may be associated with various types of potential vegetation regardless of location in the territory. In such situations, vegetation appears randomly distributed. However, this phenomenon is not considered to be important in the study area (Grimm, 1984; McCune & Allen, 1985; Messaoud *et al.*, 2007).

Climate as a sub-dominant driver

In this study, the fraction of vegetation variation explained by climate alone is very small, because changes of this set along ecological gradients are always accompanied by changes in other sets. Climate in combination with other sets of explanatory variables ranks close to combinations involving natural disturbances, which suggests that climate could be considered as a subdominant set. This subdominance is mainly defined by three combinations (two triple and the quadruple) involving climate. The combination of climate and natural disturbances, often favoured by paleoecologists (e.g., Payette *et al.*, 1989), and the double combination of physical environment and climate, which is typical of regions dominated by late-successional species and low fire frequency (e.g., Swanson *et al.*, 1988), explain a low proportion of variation. These sets become more important when considered in a triple or quadruple combination. Climate would likely be the most important factor in territories that are much larger than our study area, such as the total area covered by boreal and temperate forest in the province of Quebec (Grondin *et al.*, 2007).

1.7 Conclusion

This study explored the role of four sets of explanatory variables (drivers) in explaining the landscape heterogeneity of the boreal forest. We established a link between gradient analysis, which has a long history in vegetation science (Whittaker, 1967), and more recent developments concerning numerical ecology (RDA and partial RDA - Borcard *et al.*, 1992; Legendre *et al.*, 2005; Legendre & Legendre, 2012; Dray *et al.*, 2012). We used three vegetation themes (n=36 response variables) and four sets of factors (n=44 explanatory variables), including human disturbances, to provide a complete description of ecological gradients and their overlap for a large portion of the Canadian boreal forest (175 000 km^2). Even if fire is the main disturbance controlling the forest dynamics in boreal forest (Heinselman 1973; Rowe & Scotter 1973; Payette 1992), the global heterogeneity, defined by the links between environmental variables and vegetation, is caused by the integration of several sets of explanatory variables (drivers). Our findings show the variability of vegetation themes in regard to sets of explanatory variables, the integration of drivers and the significant role of human disturbances in explaining landscape heterogeneity. We estimate that the processes characterizing the study area resemble those at work in numerous landscapes across the biomes of the world. The structured nature of landscape heterogeneity justifies the subdivision of the study area into relatively homogeneous landscape units for finer-scale analysis (Grondin *et al.*, 2014, Grondin 2014), as well as for development of regional strategies regarding biological diversity, conservation, forest management, and the effects of global climate change.

1.8 Acknowledgements

Data sources (plots, maps) used in this study were collected by staff of the Ministère des Ressources naturelles du Québec (MRN), from 1970 to 2000. We are grateful to all these anonymous forest workers and cartographers. The present study was funded by the MRN. Comments by Dominique Arseneault, Yan Boucher, Daniel Gagnon, Brian Harvey, Paul Jasinski, Jason Laflamme, Del Meidinger, Germain Mercier, Frederic Raulier, Heloise Rheault and two anonymous reviewers as well as style revision by Denise Tousignant and Karen Grislis, were all greatly appreciated. Our thanks to Jean Noël and Véronique Poirier for their daily assistance in data analysis and geomatics.

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Table 1.1 Codes used to describe groups (prefix G) of vegetation variables and groups of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]). Each group is composed of some variables presented in Appendices 1 and 2.

Groups of response variables

GAcruS	Relative proportion of basal area for *Acer rubrum*
GBepaF	Relative proportion of area for *Betula papyrifera* forest type
GAbbaS	Relative proportion of basal area for *Abies balsamea*
GPimaAbbaF	Relative proportion of area for *Picea mariana and Abies balsamea* forest type
GPotrF	Relative proportion of area for *Populus tremuloides* forest type
GPotrPimaF	Relative proportion of area for *Populus tremuloides* and *Picea mariana* forest type
GPibaF	Relative proportion of area for *Pinus banksiana* forest type
GWetland	Relative proportion of area for non-forested wetlands
GPimaF	Relative proportion of area for *Picea mariana* forest type

Groups of explanatory variables

GGdd	C - Annual number of growing degree-days
GSbom	ND - Relative proportion of area covered by light spruce budworm outbreaks
GLog1	HD - Relative proportion of area covered by logging during the 1970 period
GEle	PE - Relief amplitude: difference in elevation between upper and lower portions of the landscape (m)
GHf1	HD -Number of human-caused fires per 100 km^2 during the 1938-1998 period
GAri	C - Aridity index
G1921f	ND - Relative proportion of plots originating from fires between 1901 and 1930
GD_4ga	PE - Relative proportion of area covered by glaciolacustrine fine-textured (clay) surficial deposits
G1891f	ND - Relative proportion of plots originating from fires between 1870 and 1900
G1851f	ND - Relative proportion of plots originating from fires before 1870
GD_7	PE - Relative proportion of area covered by organic deposits

Table 1.2 Detailed view of the relative proportion of vegetation variation (%) explained by four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to three vegetation themes. Partial canonical analysis (Y- and X-matrices) estimates the total explained and unexplained variation. The explained variation is divided into 15 fractions (Figure 2B). The unique fractions (e.g., PEu) are associated with only one set of explanatory variables, while the common fractions (e.g., PE∩C) are associated with more than one set. The common relative variation by a set is the sum of double, triple, and quadruple fractions containing this set (e.g., PEc = [PE∩C]+[PE∩HD]+[PE∩ND]+[PE∩C∩ND]+[PE∩HD∩C]+[PE∩HD∩ND]+ [PE∩HD∩ND∩C] - 7 fractions). The total relative variation by a set is the sum of unique and common fractions (e.g., [PEt]=[PEu]+[PEc] - 8 fractions). See also Figure 4 for a synthetic presentation of the results.

	Vegetation theme		
	Tree species	Forest type	Potential vegetation-successional stage
Total variation			
Explained	58.3	69.4	55.5
Unexplained	41.7	30.6	44.5
Relative proportion of explained variation (15 fractions)			
Unique variation			
Cu	2.7	4.0	2.3
NDu	25.5	11.6	36.7
PEu	7.1	13.2	2.7
HDu	3.9	2.7	3.2
Common variation			
PE∩ND	9.6	11.4	8.7
PE∩C	3.0	6.4	0.5
C∩ND	5.6	6.3	7.0
PE∩C∩ND	14.8	15.8	12.3
PE∩HD	2.0	3.1	0.4
C∩HD	1.5	1.7	1.1
HD∩ND	5.4	4.4	5.0
HD∩ND∩C	10.1	7.0	9.7
PE∩HD∩C	1.7	2.2	0.8
PE∩HD∩ND	0.4	0.8	1.1
PE∩HD∩ND∩C	6.6	9.3	6.6
Explained variation	100.0	100.0	100.0
Sums of relative proportion of explained variation			
Total unique relative variation	39.3	31.5	45.0
Total common relative variation	60.7	68.5	55.0
Total relative variation by set			
Ct	44.4	51.0	41.0
NDt	77.9	66.7	89.1
PEt	45.3	62.3	34.9
HDt	31.6	31.2	29.8
Common relative variation by set			
Cc	41.8	47.0	38.7
NDc	52.4	55.1	52.4
PEc	38.1	49.0	32.2
HDc	27.7	28.5	26.6
Double and triple variation - PE∩ND	24.5	27.3	21.0
Double and triple variation - HD∩ND	15.5	11.5	14.7

Table 1.3 R^2_{adj} for each vegetation theme in relation to four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]).

	Vegetation theme		
$R^2_{adj.}$ (%)	Tree species	Forest types	Potential vegetation-successional stages
C	26.7	36.5	23.4
ND	45.3	46.3	49.4
PE	26.8	43.5	20.2
HD	18.5	21.7	16.6

Figure 1.1 Location of the study area (outlined in red) according to the Ecological Land Classification Hierarchy of the Ministère des Ressources naturelles du Québec (Saucier *et al.*, 2009).

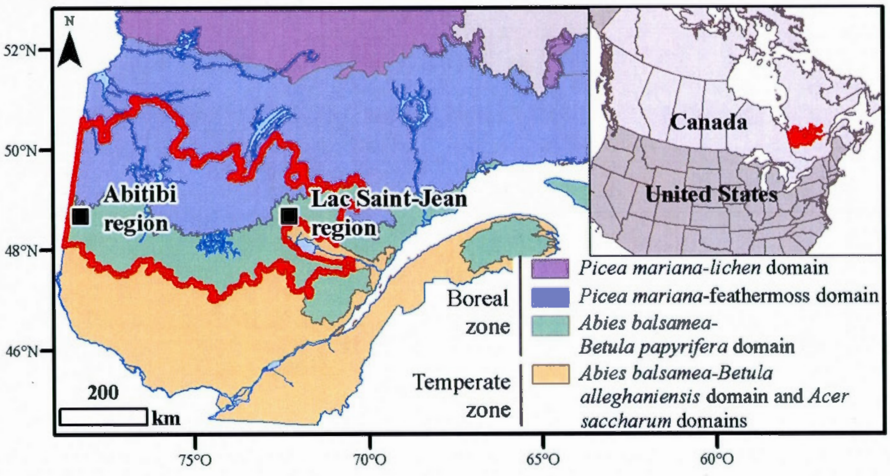
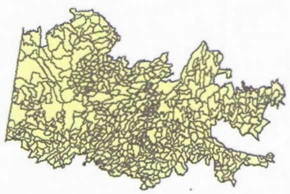


Figure 1.2 Method used A) to define the ecological gradients and B) to quantify the overlap for each of the three vegetation themes (tree species, forest types, potential vegetations–successional stages) relative to four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE] and human disturbances [HD]).

A. Ecological gradients

A1. 606 ecological districts (objects)



↓ A2. Y-matrix (three vegetation themes) ↓

↓ A2. X-matrix (four sets of explanatory variables) ↓

A3. Redundancy analysis (RDA)

↓

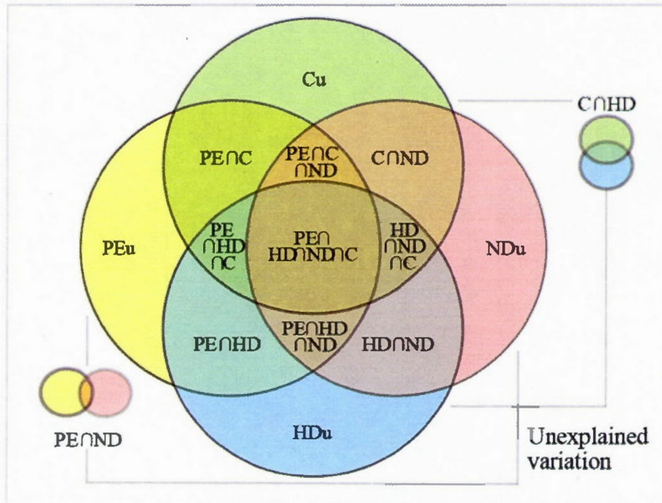
A4. *k*-means cluster analysis on canonical axes of the RDA and formation of groups of vegetation variables and groups of explanatory variables

↓

A5. Ordination diagram of groups of vegetation variables (Figure 3B) and groups of explanatory variables (Figure 3C)

B. Quantification of the overlap

Venn diagram of the variation partitioning of a vegetation theme explained by four sets of explanatory variables. The rectangle represents the total variation of Y (15 fractions of explained variation).



C: climate
PE: physical environment
ND: natural disturbances
HD: human disturbances
PEu...: unique variation
PE∩C...: double common variation
PE∩HD∩C...: triple common variation
PE∩HD∩ND∩C...: quadruple common variation

Figure 1.3 Distribution maps of variables for vegetation themes (A) and sets of explanatory variables (D), and ordination diagrams of vegetation theme variables (B) and sets of explanatory variables (C). On each map, the abundance of the variable is proportional to the darkness of the shade of gray. On the ordination diagrams, arrows indicate the direction of change, with their length reflecting their importance in structuring the landscape heterogeneity of the study area. Each group of variables is characterized by an ecological gradient (latitudinal |, latitudinal-oblique \, or longitudinal —) deduced from the distribution of the variables. The groups of variables are defined in Table 1.1.

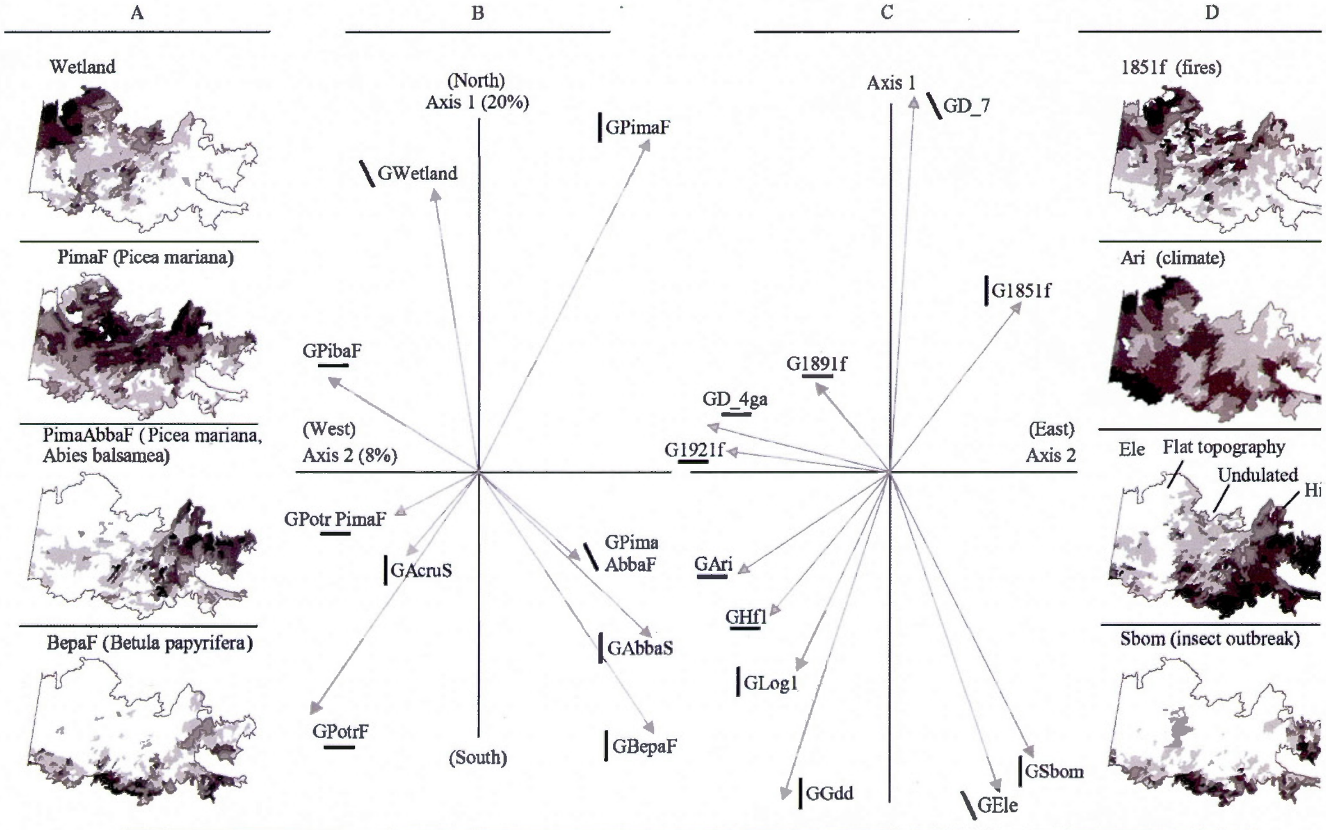


Figure 1.4 Synthetic view of the relative proportion of variation (%) explained by each of the four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to three vegetation themes. The variation is defined by the common and unique fractions illustrated in Figure 1.2B and described in Table 1.2.

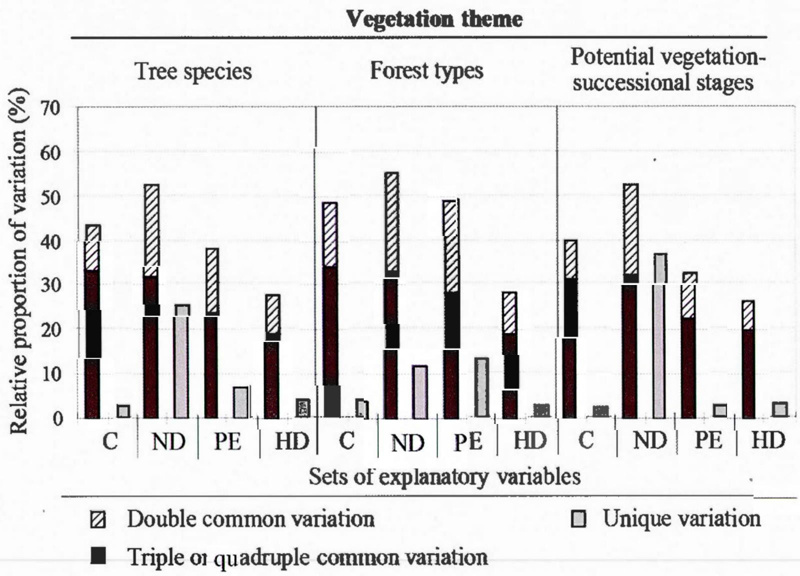
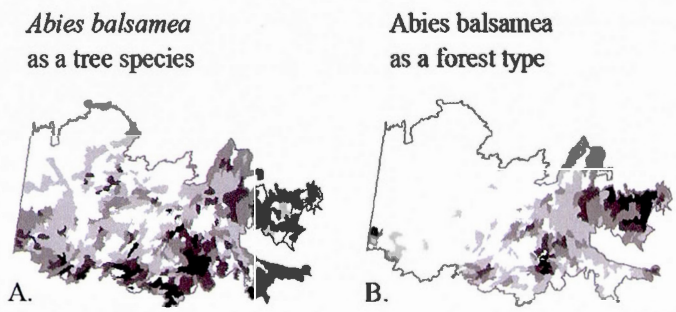


Figure 1.5 Vegetation heterogeneity according to vegetation themes. The tree species theme follows a latitudinal gradient in close association with the distribution of elements composing this theme, such as *Abies balsamea* as a tree species (AbbaS, A). The forest types theme follows a latitudinal-oblique gradient in close association with the distribution of elements composing this theme, such as the *Abies balsamea* forest type (AbbaF, B). On each map, the abundance of the variable is proportional to the darkness of the shade of gray.



1.10 Appendices

Appendix 1. Definition of response variables by theme (Y-matrix)

Appendix 2. Definition of explanatory variables by set (X-matrix)

Appendix 3. Overlap of vegetation themes and sets of explanatory variables

Appendix 4. Variables forming the parsimonious X-matrices developed for each vegetation theme (X-PE.pars, X-ND.pars, X-C.pars, X-ND'.pars)

APPENDIX 1

This appendix provides more information on the response variables used in this study and gathered in a Y-matrix (Legendre & Legendre 2012). The Y-matrix contains response variables for three vegetation themes (total m = 36 variables): tree species (m = 10), forest types (m = 14), and potential vegetations-successional stages (m = 12) (Appendix 1A). Most of the variables describe a relative proportion of forest inventory plots (tree species, potential vegetations-successional stages) or a relative proportion of area (forest types).

1- The first theme: tree species

The description of the first theme (tree species) is based on forest inventory plots (n = 53 635) conducted by the Ministère des Ressources naturelles du Québec (MRN) from 1970 to 2000 (Bard *et al.* 1975, 1983; Letarte *et al.* 1995) (Appendix 2B). Each plot is circular (radius of 11.28 m), has an area of 400-m^2 and was measured only once (temporary plots). Within each plot, each living tree with a diameter at breast height (dbh) larger than 9 cm was measured and tallied (2 cm classes). The tree species theme describes the relative proportion of 10 tree species in each ecological district based on forest inventory plots. First, each forest inventory plot was characterized by the relative proportion of basal area occupied by each species. Second, the mean relative proportion of basal area was defined for each tree species using all plots within a specific ecological district.

2- The second theme: forest types

The description of the second theme (forest types) is based on forest cover maps (scale of 1:20 000) developed during the 1980s. Initially, the forest maps were created through photointerpretation of black and white aerial photographs (scale of 1:15840). Each forest map was accompanied by a database containing a reference number, with a description of each stand delineated on the map. The description includes information on forest type, density, height, age, disturbance type (e.g., light insect outbreaks) and surface area. Subsequently, the forest map database was integrated into a geospatial database named SIFORT-2 (Pelletier *et al.* 1996, 2007). The geospatial reference of the database lies on a spatial grid of rectangular polygons called tesseræ. Each tessera represents a segment of 15 seconds of latitude and 15 seconds of longitude (geographic coordinates), and covers a 14-ha area. Integration of forest information with geospatial references (latitude, longitude) was obtained by superimposing the center of each tessera onto a forest map in order to note the reference number of the forest stand and its attributes (forest type, density, etc.). This procedure was extended to all tessera and maps (scale 1: 20 000) covering the study area. A synthesis of all forest stands delineated on the forest maps led to the definition of 14 main forest types. This synthesis was based on the total area occupied by each forest type and its geographical distribution. Less-represented forest types with similar distributions were agglomerated with more abundant forest types. To characterize each of the 606 ecological districts of the study area according to the 14 main forest types, we determined the relative proportion of area covered by each forest type using all tesseræ associated to a specific forest type.

3- The third theme: potential vegetation-successional stages

The description of the third theme (potential vegetation-successional stages) is based on forest inventory plots (n = 53 635) produced since the 1970s and complemented by 7 000 recent ecological (1980-2000) inventory plots (Blouin & Berger 2005; Saucier *et al.*, 1994). To develop the Y-matrix in regard to this theme, we first characterized each plot according to its potential vegetation and successional stage on the basis of forest species. To standardize the information noted in forest inventory plots over several years, each plot was subjected to a similar key to that presented in Appendix 1B. Such keys are also presented in *Guides de reconnaissance des types écologiques* produced for the entire study area (e.g., Blouin & Berger, 2005). The successional stages have also been defined on the basis of vegetation, and specifically the shade tolerance of species. Ultimately, the potential vegetation and successional stages are characterized on the basis of vegetation. Secondly, using all plots within a specific ecological district, the relative proportion of each combination of potential vegetation–successional stage was calculated.

Three potential vegetation types were considered: *Abies balsamea-Betula papyrifera* (Ms2), *Abies balsamea-Picea mariana* (Rs2) and *Picea mariana* (Re2). Four successional stages were also identified: early-successional (S2), intermediate (S3), facies (S4), and late-successional (S5) forest types. Plots dominated by species of early stage succession belong to S2, while those dominated by late successional species form the S5 stage. Stage S1, characterizing recently burned or cut stands, is not considered because this vegetation type was not sampled. The stands of various successional stages can recover after a disturbance, developing a forest composition similar to that of its predecessor (e.g., cyclic dynamics of *Pinus banksiana* stands), or evolve until they reach the late-successional stage (e.g., successional dynamics of *Betula papyrifera* stands evolving towards *Abies balsamea* stands) (Cogbill, 1985; Foster and King, 1986; De Grandpré *et al.,* 2000; Gauthier *et al.,* 2000; Couillard *et al.,* 2012). The proportion of successional stages belonging to the same potential vegetation type varies by region. For example, *Pinus banksiana* forest stands (S2) are an important successional stage of *Picea mariana* potential vegetation (Re2) in the central portion of our study area, where many fires are centered on the year 1921. These forest stands are less common in the northern portion composed of older landscapes (fires centered on 1851) (Grondin *et al.,* 2014).

The *Abies balsamea-Betula papyrifera* potential vegetation type (Ms2) is associated with rich soils, especially thick till or thick mesic clay. The forest dynamics of this potential vegetation type are mainly characterized by successional dynamics of stands of *Betula papyrifera* (S2 stage), *Betula papyrifera-Abies balsamea* (S3), *Abies balsamea-Betula papyrifera* (S4), and *Abies balsamea* (S5). The floristic understory generally consists of *Acer spicatum* and *Dryopteris spinulosa*. Early-successional forest stands (S2, S3) dominate the landscape for the first 100-150 years after a fire and are then replaced by late-successional species (S4, S5) (Bergeron & Dubuc, 1989; Bergeron & Dansereau, 1993; Bergeron & Charron, 1994; Bergeron, 2000; Lesieur *et al.,* 2002; Gauthier *et al.,* 2010; Couillard *et al.,* 2012). In our study area, the high frequency of fires makes pure *Abies balsamea* stands (S5) rare.

The *Abies balsamea-Picea mariana* potential vegetation type (Rs2) differs from the previous type by the absence of both *Picea glauca* and rich undergrowth species (e.g., *Acer spicatum*) and by the common presence of *Pinus banksiana* and *Picea mariana*. In forest stands with a forest floor receiving abundant light, ericaceous species (e.g., *Kalmia angustifolia*) and other shrubs (e.g., *Nemopanthus mucronata*) are well-represented. This potential vegetation type's topographic position, soil richness, and possibly fire regime, are midway between Ms2 (previous section) and Re2 (next section). Early-successional stands (S2-S3) are dominated by *Betula papyrifera*, *Populus tremuloides,* and *Pinus banksiana*, while those at the late-successional stage (S4-S5) are dominated by *Abies balsamea* and *Picea mariana* (Carleton & Maycock, 1978; Gerardin, 1980; De Grandpré *et al.*, 2000; Bouchard *et al.,* 2008; Gauthier *et al.,* 2010). We have also included in the Rs2 potential vegetation the stands dominated, in their early-successional stages, by *Populus tremuloides*. These stands are mainly observed on the clay deposits that characterize the western part of the study area (Abitibi). These sites are classified within the *Picea mariana* and *Populus tremuloides* potential vegetation (ME1 codification for mixed forest with *Picea mariana*) according to the ecological classification of the MRN. Considering that the late-successional stage is composed of *Picea mariana* and *Abies balsamea*, the same species that comprise Rs2, potential vegetation ME1 can be refered to as Rs2 given a synthetic view of the study area.

The *Picea mariana* potential vegetation type (Re2) generally occurs on flat or undulating topography. Soils are poorer than those of previous potential vegetation types.

A- Soils can be well-drained and are composed of till, sand, or rock (*Picea mariana* and mosses) (Re2 according to the MRN forest classification). In these situations, undergrowth vegetation is dominated by mosses and ericaceous shrubs, including *Kalmia angustifolia* and *Ledum groenlandicum*. This potential vegetation type is mainly characterized by the following types of forest stands: *Pinus banksiana* (S2 stage), *Pinus banksiana-Picea mariana* (S3), *Picea mariana-Pinus banksiana* (S4), and *Picea mariana* (S5). Early-successional stands (S2, S3) dominate the landscape for the first 100-150 years after a fire and are then replaced by late-successional stands (Dix & Swan, 1971; Cogbill, 1985; Foster, 1985; Bergeron &

Dansereau, 1993; Harper *et al.,* 2002; Harvey *et al.,* 2002; Lesieur *et al.,* 2002; Lecomte & Bergeron, 2005). In some situations, fires can initiate a cyclic dynamic of *Pinus banksiana* stands (Harper *et al.,* 2002). This dynamic is more frequent on coarse deposits, where fire frequency is higher than on other surficial deposits (De Grandpré *et al.,* 2000). Finally, some old *Picea mariana* stands, located in landscapes without *Pinus banksiana,* are replaced by young *Picea mariana* stands according to recurrent dynamics characteristic of eastern Quebec (Gauthier *et al.,* 2010), which are also found in the study area. Moreover, as time since the last fire increases, late-successional stands (*Picea mariana*) located in relatively flat areas can be subject to paludification and decreased productivity, thereby opening the forest cover. The severity of fires in these ecosystems is the main factor affecting forest dynamics. Intense fires lead to the formation of relatively dense and productive stands. Low-intensity fires do not favor the regeneration of *Picea mariana*, so previously well-drained sites may be altered to host *Picea mariana*-lichen stands, with previously poorly-drained stands supporting *Picea mariana*-sphagnum stands (Lecomte & Bergeron, 2005; Lecomte *et al.,* 2006; Simard *et al.,* 2007).

B- Soils can be hydric and formed essentially of peat (*Picea mariana* and sphagnum) (Re3 according to the MRN forest classification). In these situations, undergrowth vegetation is dominated by *Sphagnum* species and ericaceous shrubs, including *Ledum groenlandicum* and *Chamaedaphne calyculata*. Forest cover is mainly characterized by *Larix laricina* (stage S2), *Picea mariana-Larix laricina* (S3), *Picea mariana-Larix laricina* (S4), and *Picea mariana* (S5). Early-successional stands (S2, S3) dominate the landscape for the first 100-150 years before being replaced by late-successional stands (Carleton & Maycock, 1978; Cogbill, 1985; Gauthier *et al.,* 2000; Lecomte & Bergeron, 2005). Regardless of fire severity, these ecosystems retain a thick layer of organic material (more than 40 cm, edaphic paludification; Simard *et al.,* 2007) and exhibit low productivity.

4- Grouping and description of the response variables (Y-matrix, the three themes)

To synthesize the great number of response variables (Figure 2, Appendix 1A), a *k*-means grouping was performed on all the canonical axes of the RDA related to vegetation variables (the 3 themes) (R Development Core Team, 2010 and Vegan package) in order to form 9 groups (Appendix 1D). Each of these groups is associated with one of the three ecological gradients characterizing the study area (latitudinal, latitudinal-oblique, or longitudinal). Gradients were determined according to the spatial distribution of response variables (maps) and their position on the ordination diagrams (Figure 3 and Appendix 3A). The gradients can be considered as the synthesis of each map describing a group.

- Four groups are closely related to the latitudinal gradient: AcruS (*Acer rubrum*), BepaF (*Betula papyrifera*), AbbaS (*Abies balsamea*), and PimaF (*Picea mariana*). The first three mainly characterize the southern portion of the study area. The AcruS group is restricted to the southern border of the study area. The BepaF group is well-represented in the entire southern portion. The AbbaS group has a wider distribution in the south. The PimaF group characterizes the northern portion of the study area.

- Two groups express the latitudinal-oblique gradient. The PimaAbba group (*Picea mariana-Abies balsamea*) is distributed mainly in the southeastern portion of the study area. At the opposite end of the gradient, the Wetland group becomes increasingly abundant in landscapes dominated by undulating or flat topography. Wetlands dominate the northwestern portion of the study area.

- Three groups characterize the longitudinal gradient and all are more abundant in the western portion of the study area. The PotrF group (*Populus tremuloides*) is confined to the southwestern portion of the study area, with a small extension into the southeastern portion. The PotrPimaF group (*Populus tremuloides-Picea mariana*) is more widely distributed. The PibaF group (*Pinus banksiana*) is abundant in the central and north-central portions of the study area.

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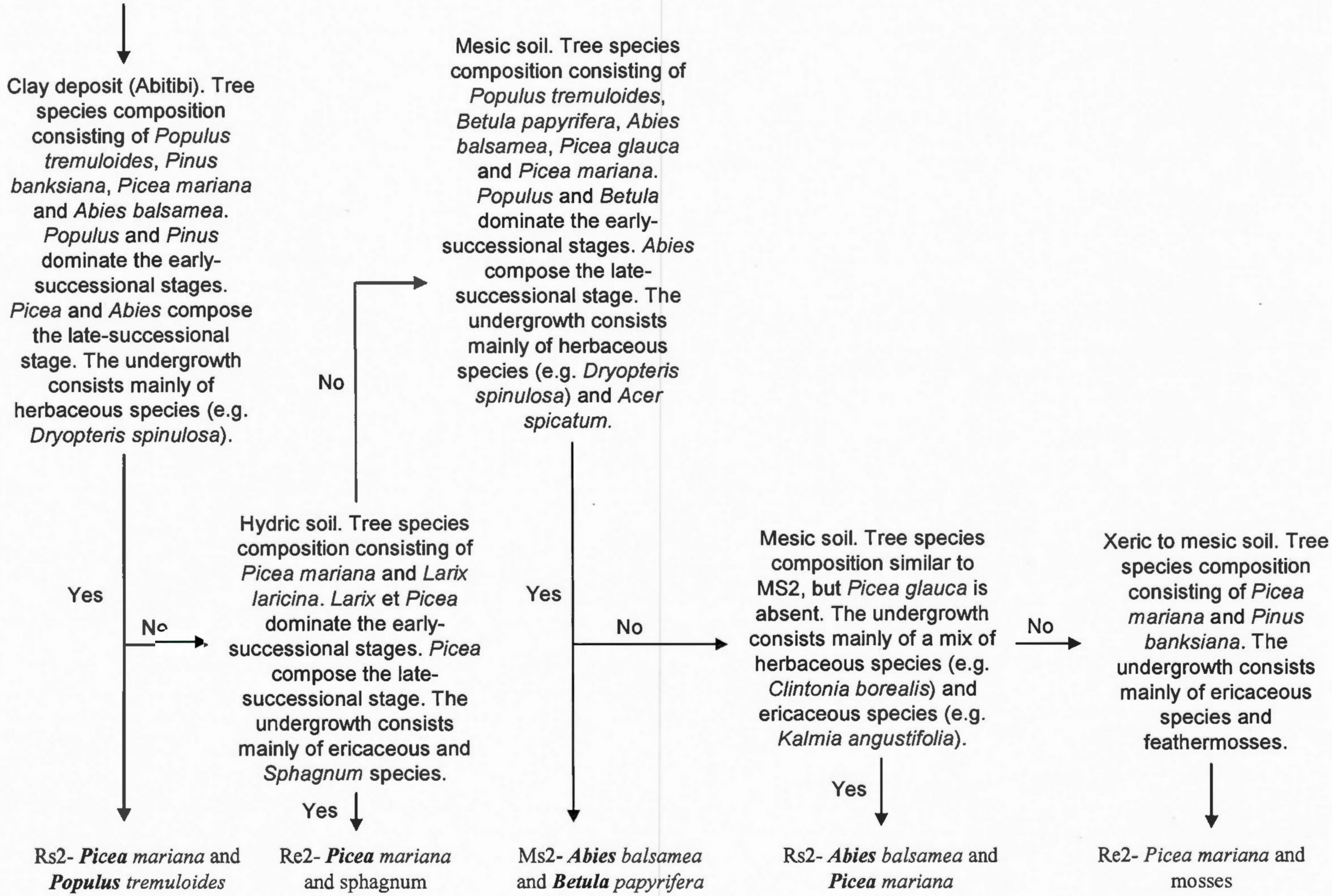
Appendix 1A. Descriptive variables and their groups

	Response variables	
Theme	Code	Description
Species[1]	BepaS	Basal area for *Betula papyrifera*
	BealS	Basal area for *Betula alleghaniensis*
	PiglS	Basal area for *Picea glauca*
	PimaS	Basal area for *Picea mariana*
	AcruS	Basal area for *Acer rubrum*
	PotrS	Basal area for *Populus tremuloides*
	PibaS	Basal area for *Pinus banksiana*
	AbbaS	Basal area for *Abies balsamea*
	SaspS	Basal area for *Salix* spp.
	ThocS	Basal area for *Thuja occidentalis*
Forest types[2]	Alru	Area for *Alnus rugosa* shrub communities
	BepaF	Area for *Betula papyrifera*
	BepaAbbaF	Area for *Betula papyrifera* and *Abies balsamea*
	BepaPimaF	Area for *Betula papyrifera* and *Picea mariana*
	BealF	Area for *Betula alleghaniensis*
	Wetland	Area for non-forested wetlands
	Heathland	Area for heathlands
	PimaF	Area for *Picea mariana*
	PimaAbbaF	Area for *Picea mariana* and *Abies balsamea*
	PibaF	Area for *Pinus banksiana*
	AbbaF	Area for *Abies balsamea*
	PotrF	Area for *Populus tremuloides*
	PotrPimaF	Area for *Populus tremuloides* and *Picea mariana*
	PotrAbbaF	Area for *Populus tremuloides* and *Abies balsamea*
Potential vegetation - successional stages[3]	Ms2S2	Plots for *Abies balsamea* - *Betula papyrifera* - early successional stage
	Ms2S3	Plots for *Abies balsamea* - *Betula papyrifera* - intermediate stage
	Ms2S4	Plots for *Abies balsamea* - *Betula papyrifera* - facies stage
	Ms2S5	Plots for *Abies balsamea* - *Betula papyrifera* - late successional stage
	Re2S2	Plots for *Picea mariana* - early successional stage
	Re2S3	Plots for *Picea mariana* - intermediate stage
	Re2S4	Plots for *Picea mariana* - facies stage
	Re2S5	Plots for *Picea mariana* - late successional stage
	Rs2S2	Plots for *Abies balsamea* - *Picea mariana* - early successional stage
	Rs2S3	Plots for *Abies balsamea* - *Picea mariana* - intermediate stage
	Rs2S4	Plots for *Abies balsamea* - *Picea mariana* - facies stage
	Rs2S5	Plots for *Abies balsamea* - *Picea mariana* - late successional stage

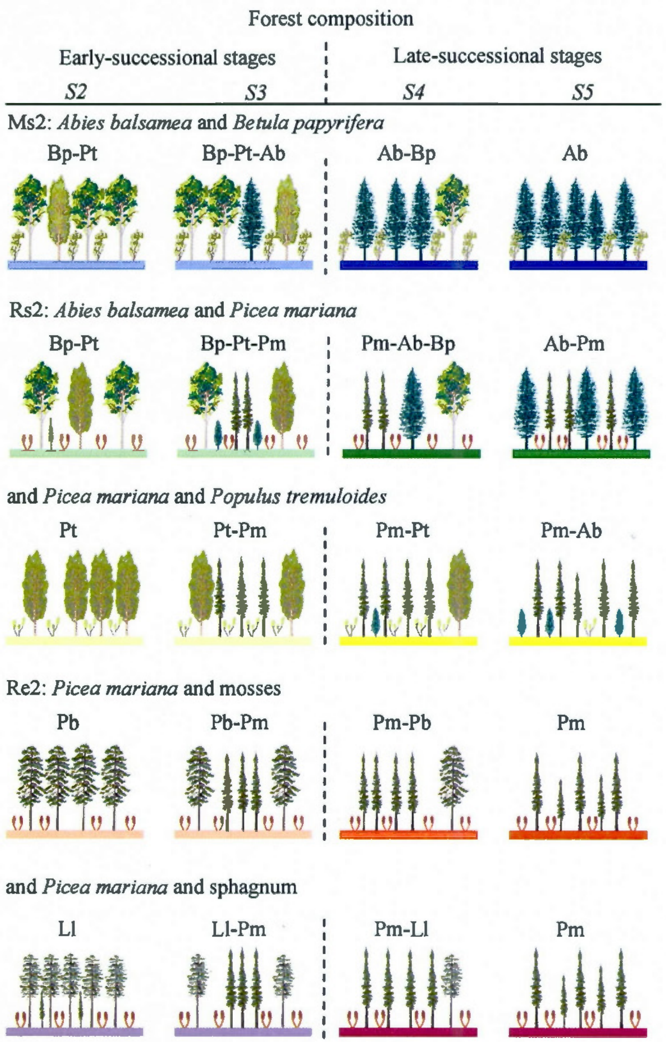
Group	Vegetation variable
GAcruS	BealF
	PotrAbbaF
	BealS
	AcruS
	ThocS
GBepaF	BepaF
	BepaAbbaF
	BepaPimaF
	BepaS
	PiglS
	Ms2S4
	Ms2S5
	Ms2S3
GAbbaS	AbbaS
	Rs2S5
GPimaAbbaF	PimaAbbaF
	AbbaF
GPotrF	PotrF
	PotrS
	Ms2S2
GPotrPimaF	Alru
	Heathland
	PotrPimaF
	SaspS
	Rs2S2
	Rs2S4
	Rs2S3
GPibaF	PibaF
	PibaS
	Re2S4
	Re2S3
GWetland	Wetland
GPimaF	PimaF
	PimaS
	Re2S2
	Re2S5

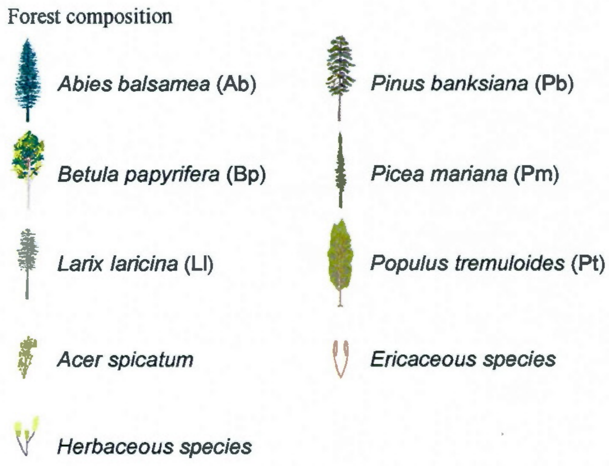
[1] Source: forest inventory plots.
[2] Source: forest maps developed during the 1980s and integrated in the SIFORT-2 geobase.
[3] Source: forest inventory and ecological plots.

Appendix 1B. Synthetic key for the identification of potential vegetation types considered in this study



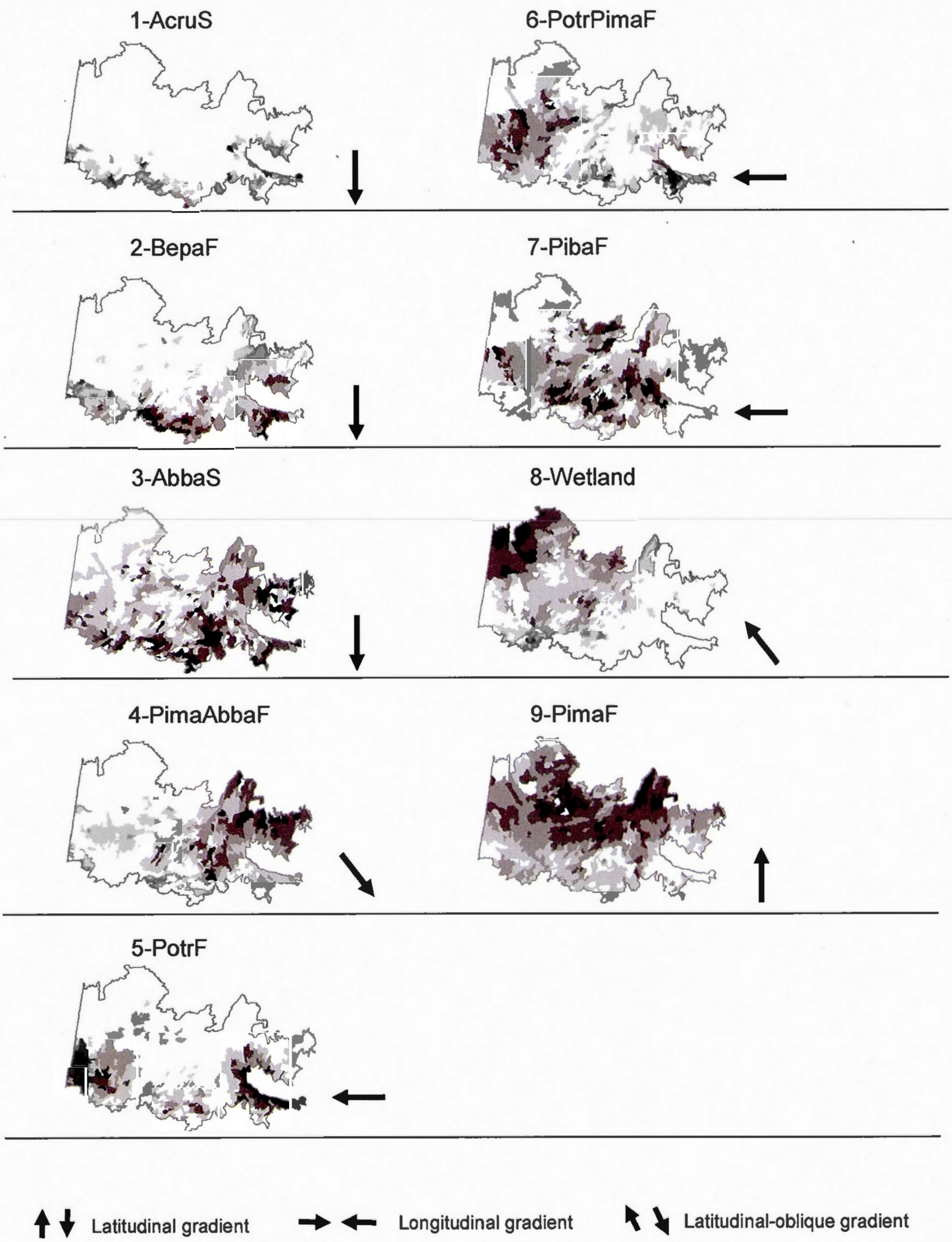
Appendix 1C. Description of potential vegetation types and their successional stages





Potential vegetation	Successional stages: Early-succession *S2-S3*	Successional stages: Late-succession *S4-S5*
***Abies** balsamea* and ***Betula** papyrifera* (Ms2)		
***Picea** mariana* and ***Populus** tremuloides* (Rs2)		
***Abies** balsamea* and ***Picea** mariana* (Rs2)		
***Picea** mariana* and mosses (Re2)		
***Picea** mariana* and sphagnum (Re2)		

Appendix 1D. Groups of vegetation variables (1-AcruS to 9-PimaF) presented according to the variable used to name the group. The darker the shade of gray, the greater the abundance of the variable. An estimate of the ecological gradients is shown near the maps. The meaning of groups of variables is presented in Appendix 1A.



APPENDIX 2

DEFINITION OF THE EXPLANATORY VARIABLES BY SET (X-MATRIX)

This appendix provides additional information on the explanatory variables used in this study and gathered in a X-matrix (Legendre & Legendre, 2012). The X-matrix contains four sets of explanatory variables (total $m = 44$ variables): climate ($m = 8$), natural disturbances ($m = 12$), physical environment ($m = 16$), and human disturbances ($m = 8$) (Appendix 2A). Most of the variables describe a relative proportion of area or a relative proportion of forest inventory plots (Appendix 2B).

1- The first set: climate

The climate (C) of each of the 606 ecological districts was characterized using the BioSIM simulator designed by the Canadian Forest Service (Régnière, 1996; Régnière & St-Amant, 2007; Régnière *et al.,* 2014). Climatic variables were estimated for the center of each ecological district for the 1961--1990 period, based on observations from 37 meteorological stations throughout the study area (Appendix 2C). Data from four weather stations closest to each sampling location were used to define the climate, after compensating for differences in latitude, longitude and elevation using the BioSIM system. The choice of four stations is based on the mean absolute error obtained when this large a number of stations is considered and our goal of preserving a local description of the climatic variables for each ecological districts. Climate was calculated for the 1961-1990 period from 30 years of Environment Canada's daily weather data (Régnière *et al.,* 2014). Some variables describe the temperature regime (Gdd, Ef, Dwfc, Dwf, Mat, Appendix 2A), and others, rainfall (Ari, Vpd, Preci). The annual number of growing degree-days (Gdd) is the year sum of average daily temperatures, cumulative for the days on which the average temperature was > 5 C. The aridity index (Ari) corresponds to the sum of the monthly water deficits based on the difference between monthly precipitation and Thornthwaite potential evapotranspiration. The vapor pressure deficit (Vpd) is the difference (deficit) between the amount of moisture in the air and how much moisture the air can hold when it is saturated. This variable is expressed in millibars (mbar).

2- The second set: natural disturbances

Natural disturbances (ND) were described relative to the contemporary history (the last 150 years) of fires and spruce budworm outbreaks. The SIFORT-2 geospatial database provided data for variables describing the relative proportion of each ecological district affected by light insect outbreaks (Sbom), severe insect outbreaks (Sbos), windthrow (Wi), and natural fires (Fia). The number of years of infestation by spruce budworm (Sbon) and the frequency of fires per 100 km^2 (Fif) from 1938 to 1998 were described from archived data concerning natural and human disturbances (anhd) available from the Ministère des Ressources naturelles du Québec (MRN). The forest inventory plots provided information about the period and type of disturbance (fire, spruce budworm outbreaks). In each plot, three dominant or codominant trees were selected to calculate age and total height. Selected trees were cored at 1 m above the root collar in order to count the number of annual growth rings. Each plot was ascribed an age based on the oldest tree studied (based on the ring counts of three mature trees). These ages were standardized to obtain the age in 2000. Age data shows that natural disturbances were centered on four distinct periods: 1851 (origin prior to 1870), 1891 (1871-1900), 1921 (1901-1930) and 1951 (1930 and later). These periods were established by comparing the distribution and abundance of the plots classified by 10-year periods. Similar decades were pooled. This procedure explains why periods do not have the same duration. Each plot was also classified according to type of disturbance, based on 1) forest composition and 2) maps of natural disturbances (fires). Post-fire forest types formed categories (1851f, 1891f, 1921f) different from those following spruce budworm outbreaks (1851o, 1891o, 1921o). All the plots dominated by early-successional species, such as *Pinus* *banksiana* and *Betula papyrifera,* were associated with fires. By contrast, plots dominated by *Abies balsamea* were classified according to insect outbreaks dynamics. The proportion of plots belonging to the 1951 period and located in the area covered by logging (log1) were added to that of the 1851 period because we estimated that a large proportion of stands associated to the 1951 period originated from logging conducted in old stands (Grondin 2014). For each of the 606 ecological districts, the relative proportion of plots dating from a specific period and type of origin (e.g., 1921o) was calculated using all plots.

3- The third set: physical environment

Physical environment (PE) was described using a MRN database containing information on each ecological district, including the relative proportion of surficial deposits and physiographic variables (e.g., mean altitude) (Saucier *et al.,* 1994; Robitaille & Saucier, 1998).

4- The fourth set: human disturbances

Human disturbances (HD) were analyzed mainly on the basis of the SIFORT-1 and SIFORT-2 geospatial databases, which used forest maps from the 1970s and 1980s, respectively. The SIFORT-1 database was developed following the same procedure as that described above for SIFORT 2 (see forest type theme). The relative proportions of the area covered by agriculture, fallow land, logging, and human–induced fires (as well as frequency for this last variable) were calculated from all tesserae in each of the 606 ecological districts. Because of the close correspondence between logging and forests originating from the period centered on 1951, these last forests were considered in the set of human disturbances when located in a logging area (Appendix 2D, Log1). According to the forest inventory plots (fip), stands dating to the period centered on 1951 are relatively rare (less than 10%), except in the landscapes affected by human activities (Grondin *et al.*, 2014).

5- Grouping and description of the explanatory variables (X-matrix, the four sets)

To synthesize the great number of explanatory variables (Figure 2, Appendix 2A), a *k*-means grouping was performed on all the canonical axes of the RDA related to explanatory variables (the 4 sets) (Figure 2, R Development Core Team, 2010 and Vegan package) in order to form 11 groups (Figure 3, Appendix 2D). Each of these groups occupies a specific portion of the study area and is associated to one of the three ecological gradients characterizing the study area (latitudinal, latitudinal-oblique, longitudinal). Gradients were determined according to the spatial distribution of explanatory variables (maps) and their position on the ordination diagrams (Figure 3 and Appendix 3B). The gradients can be considered as the synthesis of each map describing a group (Appendix 2D).

- Three groups are closely related to the physical environment set of explanatory variables: Ele, D_7, and D_4ga. The first two groups have an opposite distribution along the latitudinal-oblique gradient. The third group is restricted to the western position of the study area and is related to the longitudinal gradient.
- Four groups describe the diversity of the natural disturbances. Two of these, Sbom and 1851f, are strongly related to the latitudinal gradient. Sbom characterizes the southern portion of the study area and 1851f, the northern portion. Groups 1921f and 1891f are mainly observed in the central portion. 1921f is more abundant in the western portion of the study area and 1891f in the western-central portion; both groups belong mainly to the latitudinal gradient.
- Two groups are associated to climate. The first, Gdd, includes the variables characterizing the latitudinal gradient. The second, Ari, is composed of variables associated with the longitudinal gradient.
- Two groups also describe human disturbances. The first, Log1, characterizes the human activities that occurred in the southern portion of the study area and is

associated with the latitudinal gradient. The second, Hf1, relates to the variables characterizing mainly the southwestern portion of the study area and, to a lesser extent, the southeastern portion. The longitudinal gradient is associated with this group.

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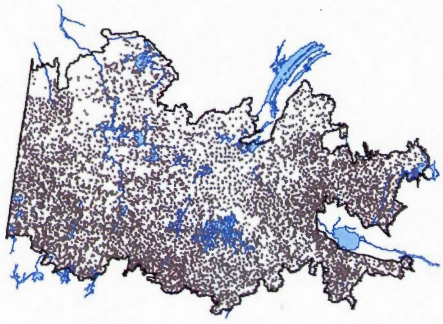
Appendix 2A. Explanatory variables and their groups. Data sources: anhd: archival data of natural and human disturbances; bios: BioSIM software; ded: database of ecological districts; fip: forest inventory plots, gs1: geospatial database Sifort-1; gs2: geospatial database Sifort-2; sfl: shape files of lakes.

	Explanatory variables	
Set	Code	Description and data source
Physical environment	Malt	Mean altitude (m) (ded)
	Ele	Absolute difference of topographic elevation (m) (ded)
	D_wa	Relative proportion of area covered by water (ded)
	D_4ga	Area covered by glaciolacustrine fine-textured (clay) surficial deposits (ded)
	D_4gs	Area covered by glaciolacustrine coarse-textured (sand) surficial deposits (ded)
	D_2a	Area covered by juxtaglacial deposits (ded)
	D_2b	Area covered by proglacial deposits (ded)
	D_7	Area covered by organic deposits (ded)
	S_a	Area covered by slopes below 4% (ded)
	S_b	Area covered by slopes ranging from 4 to 8% (ded)
	S_c	Area covered by slopes ranging from 9 to 15% (ded)
	S_d	Area covered by slopes over 15% (ded)
	D_1a	Area covered by thick till (more than 1m) (ded)
	D_1ar	Area covered by thin till (less than 1m) (ded)
	D_r	Area covered by rock (ded)
	L_100 km^2	Mean number of lakes per 100 km^2 (sfl)
Natural disturbances	1851o	Plots originating from spruce budworm outbreaks before 1870 (fip)
	1851f	Plots originating from fires before 1870 (fip)
	1891o	Plots originating from spruce budworm outbreaks between 1870 and 1900 (fip)
	1891f	Plots originating from fires between 1870 and 1900 (fip)
	1921o	Plots originating from spruce budworm outbreaks between 1901 and 1930 (fip)
	1921f	Plots originating from fires between 1901 and 1930 (fip)
	Fia	Area covered by natural fires (gs2)
	Wi	Area covered by windthrow (gs2)
	Sbom	Area covered by light spruce budworm outbreaks (gs2)
	Sbos	Area covered by severe spruce budworm outbreaks (gs2)
	Fif	Frequency of natural fires per 100 km^2 from 1938 to 1998 (anhd)
	Sbon	Number of years of infestation by spruce budworm from 1938 to 1998 (anhd)
Climate	Ari	Aridity index (bios)
	Gdd	Annual number of growing degree-days (bios)
	Vpd	Vapor pressure deficit (total daily deficit (in Mbar) from June to August) (bios)
	Ef	Early frost (Julian day corresponding to the first frost) (bios)
	Dwfc	Number of consecutive days without freezing (bios)
	Dwf	Total number of days without freezing (bios)
	Preci	Rainfall during the growing season (mm) (bios)
	Mat	Annual average temperature (bios)
Human disturbances	Ag1	Area covered by agriculture during the 1970s (gs1)
	Ag2	Area covered by agriculture during the 1980s (gs2)
	Log1	Area covered by logging during the 1970s (gs1)
	Log2	Area covered by logging during the 1980s (gs2)
	Hf1	Frequency of human-caused fires per 100 km^2 from 1938 to 1998 (anhd)
	Hf2	Area covered by human-caused fires from 1938 to 1998 (anhd)
	Fa1	Area covered by fallow land (gs1)
	1951	Relative proportion of stands originating later than 1930 (fip)

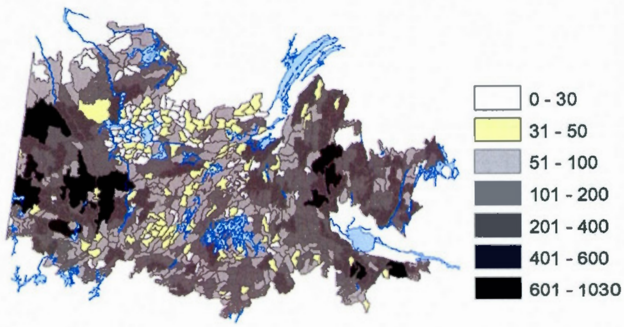
Group	Explanatory variables
GGdd	Dwfc
	Mat
	Gdd
	Dwf
	Ef
GSbom	Sbon
	Sbom
	1921o
	Sbos
GLog1	Log2
	1951
	Log1
	Hf2
GEle	D_r
	L_100 km^2
	D_1a
	D_2a
	D_2b
	D_1ar
	Ele
	S_b
	S_c
	S_d
	Malt
	Preci
	1851o
	1891o
	Fif
GHf1	Ag1
	Fa1
	Ag2
	Hf1
GAri	Vpd
	Ari
G1921f	1921f
GD_4ga	D_4gs
	D_4ga
G1891f	D_wa
	1891f
G1851f	1851f
	Wi
	Fia
GD_7	S_a
	D_7

Appendix 2B. Forest inventory plots established by the Ministère des Ressources naturelles du Québec (MRN) and used to describe some vegetation themes and explanatory variables. These plots were produced between 1970 and 2000 (n = 53 635).

Distribution of plots

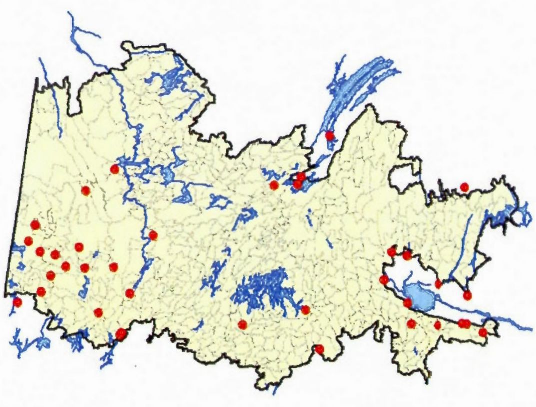


Number of plots by ecological district

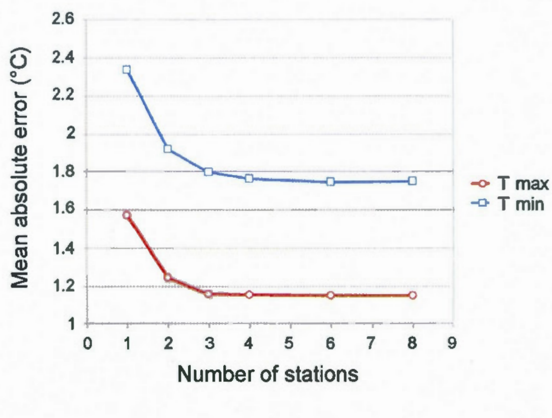


Appendix 2C. Climate

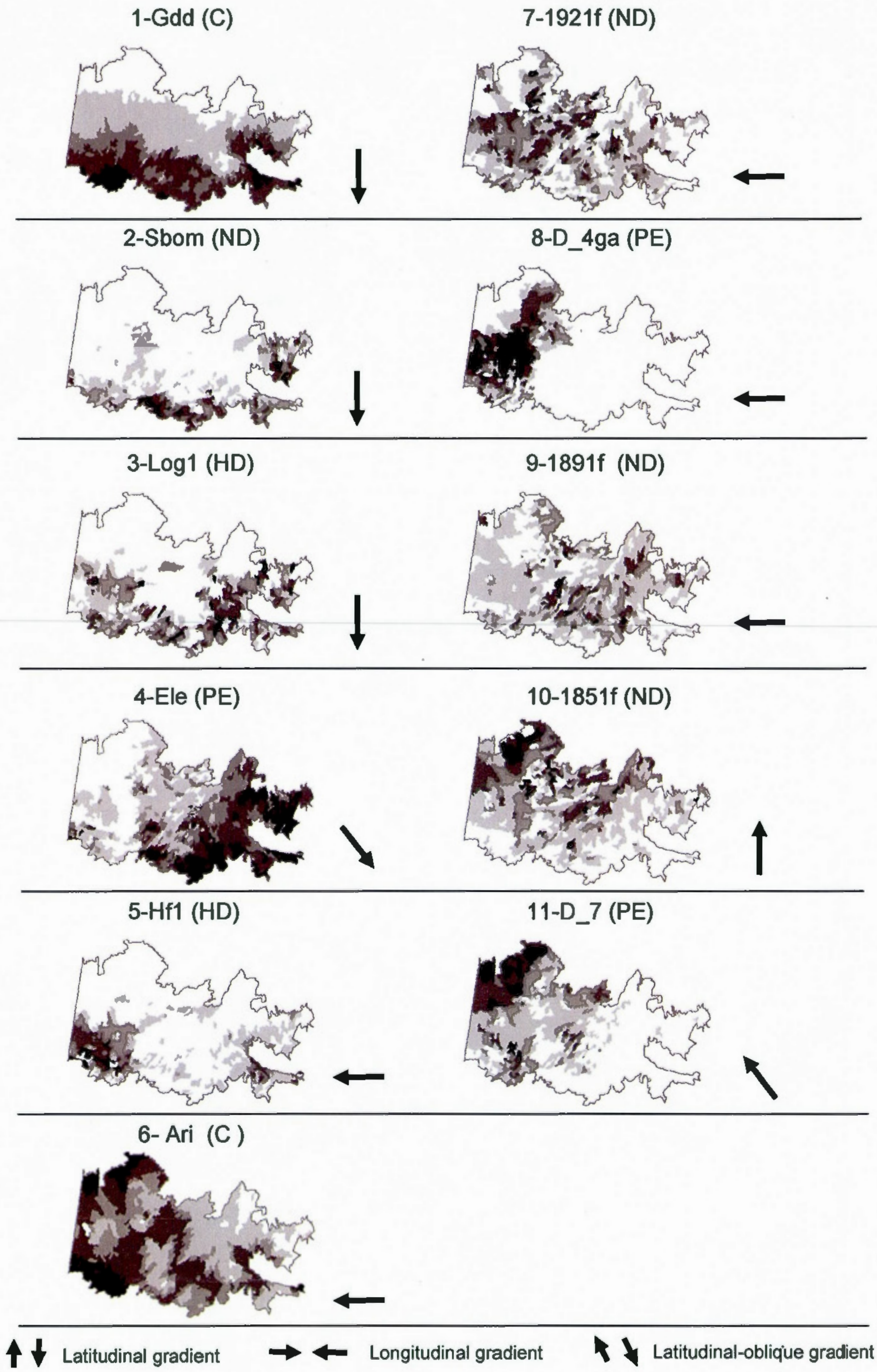
Distribution of the meteorological stations used to describe the climatic explanatory variables across the study area



Mean absolute error (°C) according to the number of meteorological stations



Appendix 2D. Groups of explanatory variables (1-Gdd to 11-D_7) presented according to the variable used to name the group. The darker the shade of gray, the greater the abundance of the variable. An estimate of the ecological gradients is shown near the maps. The meaning of groups of variables is presented in Appendix 2A.



APPENDIX 3

OVERLAP OF VEGETATION THEMES AND SETS OF EXPLANATORY VARIABLES

3.1 General description of the overlap

This study is composed of three main sections: 1) describing the ecological gradients, 2) understanding of the overlap between response and explanatory variables and 3) quantifying the overlap by using variation partitioning. In the main part of the article, sections 1 and 3 have been discussed. The overlap was briefly presented at the end of the second section in Figure 3. This appendix provides more information on the overlap, considered as an important step to interpret the results of the variation partitioning. To characterize the overlap, we defined geographical units for each vegetation theme and each set of explanatory variables and used their location on ordination diagrams to examine the overlap between the 2 types of data (Appendices 3A, 3B). To define geographical units, separate *k*-means cluster analyses were carried out on raw data from each vegetation theme and each set of explanatory variables. Vegetation data characterizing each ecological district was subjected to Hellinger transformation prior to clustering. More specifically, each of the abundance values of a site was divided by the sum of the abundance values of the entire site, then made the square root of this value$\sqrt{\frac{y_{1j}}{y_{1+}}}$. Hellinger minimizes the effect of double-zeros, it flattened the data, attenuated their relative weight. The final number of clusters was based on the Calinski-Harabasz criterion (Borcard *et al.,* 2011) and on our knowledge of descriptive and explanatory variables. Calinski-Harabasz criterion is the ratio between the sum of square between-cluster/sum of square within-cluster. The ecological districts belonging to each geographical unit were related to the canonical axes of the RDA used to describe the ecological gradients (Figure 2). More specifically, the centroids of each geographical unit were superimposed on ordination diagrams. Appendices 3A, 3B).

Ordination diagrams make it possible to compare the geographical units of the three vegetation themes (Appendix 3A) with those of the four sets of explanatory variables (Appendix 3B). On both ordination diagrams, axis 1 is vertical and axis 3 is horizontal, to reflect the geographical organization of the territory. Here, axis 3 was given precedence over axis 2, because it best describes the latitudinal-oblique gradient (Grondin *et al.,* 2014). Below are a few key observations regarding the overlap between the vegetation themes and sets of explanatory variables.

1- Geographical unit F1 (Appendix 3AA) of the forest type theme, located in the southeastern part of the study area, is characterized by a high abundance of the *Betula papyrifera* group (GBepaF) (Appendix 3AB). Unit F1 has affinities with unit F2 of the same theme and also with units belonging to other themes (PV1-2, S1) (Appendix 3AB). These affinities are highlighted by the close orthogonal projections of the unit centroids on the vegetation variable vectors (Legendre & Legendre, 2012).

2- The relationship between unit F1 on the first ordination (Appendix 3AB) and the explanatory variables can be established by analyzing the corresponding portion of the second ordination (Appendix 3BB), which shows that unit F1 is closely related to four explanatory variables: 1) GGdd (climate: highest annual number of growing degree-days), 2) GSbom (natural disturbances: high proportion of area covered by a light spruce budworm outbreak), 3) GEle (physical environment: hilly topography), and 4) GLog1 (high proportion of area affected by logging). There are also links between F1 and some geographical units of explanatory variables, more specifically C1, ND1, HD1, and PE1 (Appendix 3BB). All these elements characterize the southeastern portion of the study area. The fact that the same position is occupied by vegetation variables and their geographical units on the first ordination, and by explanatory variables and their geographical units on the second ordination, confirms their overlap. A similar description can be made for units F2 to F6.

F2 characterizes the southwestern portion of the study area. It is related to two groups of explanatory variables (GHfl and GAri, Appendix 3BB) and two geographical units (HD2 and C2) (Appendix 3BB).

F3 is located in the central-eastern portion of the study area (Appendix 3AA), where the GPimaAbbaF vegetation group is found in abundance (Appendix 3AB, Appendix 1C). This portion is linked to some geographical units. PE2, C3, and HD3 have a more southern distribution than HD4, C4, and ND2 (Appendix 3B).

F4 characterizes the central-western portion of the study area (Appendix 3AA). Among the geographical units linked to F4, some are more closely related to the western portion. This is the case for two groups of environmental variables (G1921f, GD_4GA, Appendix 2D) and four geographical units of explanatory variables (PE3, ND4, HD5, PE6, C5, Appendix 3B). Some geographical units are located in both the western and central portions of the study area (PE5, HD6, ND3, Appendix 3B).

F5 belongs to the northeastern portion of the study area (Appendix 3AA), associated with the G1851f group of explanatory variables (fires of the 1851period) (Appendix 3BB, Appendix 2D). Geographical units C6 and ND5 are located in a more eastern position than the other units, which show affinities with the central-northern portion of the study area (ND6, HD7, C7, PE4) (Appendix 3B).

F6 is strongly associated with the northwestern portion of the study area (Appendix 3AA). Organic soils are abundant (GD_7, Appendix 3BB, Appendix 2D). Geographical units PE7, ND7, and C8 are closely related to this study area. C9 is more widely distributed (Appendix 3B).

The spatial structure of the study area, described on both ordinations (Appendices 3A, 3B), makes it possible to identify three regions closely related to those delineated by Grondin et al. (2014):

- R1 is located in the southern part of the territory. Unit F1, described above, belongs to this region.
- R2, in the center, is defined by units such as F3 (Appendix 3A). The *Picea mariana-Abies balsamea* forest type (GPimaAbbaF) is the most abundant (Appendix 3AB). The F3 geographical unit (Appendix 3AB) is first closely related to PE2 (physical environment, Appendix 3BB), characterized by a hilly topography (GEle, Appendix 2D), second to ND2, where the stands originating from the 1891 period (1891f) are important, third to C3, considered as a relatively mild and wet climate, and fourth to HD3, where much of the area is affected by recent logging (since 1970) (Appendix 3B).
- R3 corresponds to the northern part of the territory. Unit F5 (Appendix 3A), belonging to this region, is dominated by the *Picea mariana* forest type (PimaF) (Appendix 3AB). It is first closely related to the PE4 physical environment unit (Appendix 3BB), characterized by an undulated topography (Ele, Appendix 2D), second to ND5, with abundant old forests (1851f), third to C7, considered as a relatively cold climate, and fourth to HD7, defined by minimal human activities.

In regions R1 and R2, natural (ND) and human disturbances (HD) show some overlap, which is described by two combinations of groups of variables (Appendix 3B). The first associates light spruce budworm outbreaks (GSbom) and logging activities (GLog1), in close relation to the ND1 and HD1 geographical units. The second combination concerns natural fires of the 1921 period (G1921f) and human-induced fires (GHf1), which are both closely related to the ND4, HD2, and HD5 geographical units, located in the southeastern and southwestern parts of the study area.

3.2 Maps of vegetation themes

Another goal of this appendix is to provide details on the maps of vegetation themes and sets of explanatory variables (Appendices 3C, 3D). Each map is accompanied by an estimate of its gradients. For example, climate shows an important latitudinal gradient expressed by the descriptive variables of the thermal regime. The longitudinal gradient (aridity regime) should also be taken into account, due to an obvious increase in aridity and a decrease in rainfall from east to west. The gradients can be considered as the synthesis of each map.

The tree species map is composed of five geographical units (S1 to S5). Unit S1 consists mainly of *Betula papyrifera* (BepaS), *Picea mariana* (PimaS), and *Abies balsamea* (AbbaS). *Abies balsamea* (AbbaS) is well-represented and occurs regularly in hardwood and softwood stands as a subdominant or companion species. Although much more scattered, *Picea glauca* (PiglS) regularly accompanies *Abies balsamea* (AbbaS). Temperate species (BealS) are rare and at the northern limit of their distribution. Unit S2 is dominated by two forest species, *Populus tremuloides* (PotrS) and *Picea mariana* (PimaS). *Betula papyrifera* (BepaS), *Pinus banksiana* (PibaS), and *Abies balsamea* (AbbaS) are also well-represented. Unit S3 shows a dominance of *Picea mariana* (PimaS). *Abies balsamea* (AbbaS) and *Betula papyrifera* (BepaS) are other important species in these forest stands. While Unit S4 is also dominated by *Picea mariana* (PimaS), it shows an increase in *Pinus banksiana* (PibaS) and a decrease in *Abies balsamea* (AbbaS) and *Betula papyrifera* (BepaS), which distinguish it from unit S3. Finally, unit S5 is characterized by high proportions of *Picea mariana* (PimaS), with other components being sparse.

The forest types are distributed according to 6 geographical units (F1 to F6). Unit F1 consists mainly of forests dominated by *Betula papyrifera* (BepaF, BepaPimaF, BepaAbbaF). *Picea mariana* forest stands (PimaF) are relatively abundant. *Betula* *alleghaniensis* stands (BealF) are very poorly represented and are at their northern limit of distribution. Unit F2 is characterized by abundant *Populus tremuloides* stands (PotrF, PotrPimaF); *Picea mariana* stands are also well-represented. Although scarce, *Alnus rugosa* (Alnu) and well-drained areas of non-forest vegetation (heathland) reach their highest levels of cover. Unit F3 shows a marked decrease in hardwood and mixed stands to the benefit of *Picea mariana* forest stands (PimaF). *Picea mariana* and *Abies balsamea* stands (PimaAbbaF) and *Abies balsamea* stands (AbbaF) are well-represented and reach their maximum cover in the study area. *Pinus banksiana* stands (PibaF) are abundant locally. Three ecosystems dominate unit F4: *Picea mariana* stands (PimaF), *Pinus banksiana* stands (PibaF), and non-forested peatlands (Wetland). *Pinus banksiana* stands (PibaF) reach their maximum cover. F5 is dominated by *Picea mariana* stands (PimaF), with *Pinus banksiana* (PibaF) and wetlands also being well-represented. Finally, F6 is dominated by non-forested peatlands (Wetland) and *Picea mariana* stands (PimaF).

Under the theme of potential vegetation-successional stages (PV1-PV6), the study area is divided into four geographical units. Unit PV1-2 contains the most stands belonging to the *Abies balsamea* and *Betula papyrifera* potential vegetation type (Ms2), particularly in the early-successional stage (Ms2S2). Temperate elements are scattered, but can be considered a particularity of this unit; they are represented by *Abies balsamea* and *Betula alleghaniensis* (Ms1), as well as by the *Abies balsamea* and *Thuja occidentalis* (Rs1) potential vegetation types. Unit PV3-4 shows a drastic reduction of forest stands belonging to Ms2. While not dominant, Rs2 potential vegetation is more abundant than elsewhere. All successional stages (S2 to S5) are represented in equal proportions. The Re2 potential vegetation type dominates, especially in the early-successional stage (Re2S2), which is mainly represented by *Pinus banksiana* stands (PibaF) of varying ages and by *Picea mariana* stands (PimaF) of 90 years of age or less. In unit PV5, Ms2 is rare and mostly located in an area protected from frequent fires (sheltered topography). Stands belonging to Rs2 show a slight decrease in area compared to the PV3-4 unit. This favors the Re2 potential vegetation type, represented by stands of early (Re2S2) or late-successional (Re2S5) stages. Finally, unit PV6 is characterized by an increase in late-successional stands belonging to the *Picea mariana* potential vegetation type (Re2S5) and, to a lesser extent, the *Abies balsamea* and *Picea mariana* potential vegetation type (Rs2S5).

3.3 Maps of sets of explanatory variables

The physical environment is described by seven geographical units (PE1 to PE7). PE1 is marked by the greatest absolute difference between the highest and lowest elevations of an ecological district (Ele, topographic elevation) and steep slopes (S_c and S_d). The topography is hilly and thin till surficial deposits are relatively abundant. In unit PE2, the topography is less accentuated (undulated), with a lower proportion of steep slopes and an increasing proportion of thick till. Unit PE3 continues the gradation of well-expressed topography toward flattened units. The absolute difference in elevation decreases and the proportions of low slopes (S_a), thick till (D_1a), proglacial deposits (D_2b), and organic deposits (D_7) increase. Unit PE4 shows similar changes in physical environment. Low slopes (S_a) increase significantly and the topography is typically undulated. For the first time, organic deposits cover more than 10% of the unit. However, the Gouin Reservoir, which is not a naturally-occurring land feature, represents a large portion of this area. Unit PE5 forms a transition between units dominated by glacial deposits and those formed mainly by glaciolacustrine and organic deposits. The most abundant surficial deposits are glaciolacustrine fine texture (D_4ga), thick till (D_1a), and organic deposits (D_7). In this unit, the presence of rock (D_R) is generally associated with sites washed by the waves of post-glacial lakes. Unit PE6 forms a vast plain of glaciolacustrine deposits (D_4ga) interspersed with organic material (D_7). The topography is typically flat. Unit PE7 corresponds to poorly-drained lowland, clearly dominated by organic deposits (D_7, ombrotrophic peatlands).

The differing characteristics of natural disturbances make it possible to subdivide the study area into seven geographical units (ND1 to ND7). Unit ND1 is strongly associated with spruce budworm outbreaks. Nearly 20% of this area shows evidence of outbreaks, according to forest maps of the 1980s (Sbom). The mean number of years of infestation during the 1938-1998 period is close to 20 (Sbon). While most stands currently dominated or subdominated by *Abies balsamea* date back to the spruce budworm outbreak that occurred at the beginning of the last century (1921o), some date back to earlier outbreaks (1891o, 1851o). Some stands might have originated from an outbreak in the middle of the last century (1951 period), but we chose to classify all these forest stands with the set of human disturbances, because in the context of our study, it was impossible to distinguish between stands (dominated or subdominated by *Abies balsamea*) associated with insect infestation and those linked to logging. We hypothesize that only a few stands date back to the last mid-century outbreak. Unit ND2 differs from unit ND1 mainly by its fire-dependent forest dynamics. The relative proportion of stands in this unit affected by insect outbreaks (1921o, 1891o, 1851o) is close to 30%, compared to 45% in unit ND1. Many forest stands originate from fires (50%), and slightly more date back to the 1921 period (1921f) than to earlier periods (1891f, 1851f). In unit ND3, stands having reached the facies or late-successional stages (abundance of *Abies balsamea*) and affected by budworm outbreaks (1921o, 1891o, 1851o) characterize only 15% of the forest inventory plots. Furthermore, stands originating from fires of the 1921 period (1921f) are at their optimum. Unit ND4 is similar to ND3, with stands from fires of the 1921 period (1921f) still abundant. Compared to ND3, ND4 shows a decrease in stands from the 1891 period (1891f), and an increase in stands affected by insect outbreaks (1921o). Stands affected by spruce budworm (1921o) characterize the small hills of mixed forest (*Abies balsamea* and hardwood species) dispersed over the vast clay plain. Units ND5, ND6, and ND7 all have a high proportion (more than 30%) of stands that grew after the fires of the 1851 period (1851f). ND5 has some old-growth forests affected by insect outbreaks (old *Abies balsamea* forest stands in the mountains). These stands originate from several outbreaks (1921o, 1891o, and 1851o) on close to 15% of the forest inventory plots. Although the fires of the 1921 period are well-represented, they are less abundant than in unit ND6, where young stands (1921f) are also more abundant than older ones (1851f). We presume that young stands grow mainly on xeric (glaciofluvial deposits) soils and that old stands are more frequent on hydric soils. Finally, ND7 is a favourable area for old-growth forests because of the abundance of organic deposits (D_7). Stands originating from the 1851 fire period (1851f) cover more than 40% of the unit.

The climate of the study area was divided into nine geographical units (C1 to C9). Unit C1 is characterized by a relatively high mean annual temperature (Mat), a high annual number of growing degree-days (Gdd), a high number of days without frost (Dwf, Dwfc), and abundant rainfall (Preci). Unit C2 has a thermal balance similar to C1. However, since it is located at the southwestern portion of the study area, aridity (Ari) and vapor pressure deficit (Vpd) are relatively high, and rainfall (Preci) is relatively low. Units C3, C4, and C5, forming the central portion of the study area, are colder than the previous ones. Their mean annual temperature (Mat) is between 0 and 1°C, with 1200 to 1300 annual growing degree-days (Gdd) and 90 to 95 consecutive days without freezing (Dwfc). The main differences between units C3, C4, and C5, which characterize the longitudinal gradient, are 1) an increase in aridity index (Ari) and vapor pressure deficit (Vpd), and 2) a decrease in precipitation (Preci). Units C6, C7, C8, and C9, forming the northern portion of the study area, are colder than the others. The mean annual temperature (Mat) is below 0 °C, the annual number of growing degree-days (Gdd) is generally below 1200, and the number of consecutive days without freezing (Dwfc) is less than 90. The main differences between units C6, C7, and C8, which characterize the longitudinal gradient, are an increase in aridity index (Ari) and vapor pressure deficit (Vpd), and a decrease in precipitation (Preci). The longitudinal weather gradient is not observed in unit C9.

Human disturbances define seven geographical units (HD1 to HD7). HD1 has been affected by logging for at least 70 years (1951, Log1, Log2). The variable 1951 indicates the relative proportion of plots with the oldest tree dating back no further than 1930, when intensive logging began in the study area (meaning that the oldest tree was younger than 70 years old in 2000). In HD1, forest stands originating from the 1951 period are present but not significant (close to 10%). About 15% of the area is affected by logging, both on the first forest maps used (1970 period, SIFORT-1) and on more recent maps (1980 period, SIFORT-2). In unit HD2, on the other hand, agriculture (Ag1, Ag2) and fallow lands define an agro-forest landscape. The frequency of human-induced fire (Hf1) reaches its highest values. The relative proportion of the area affected by human activities during the 1938-1988 period is high (HF2), but the impact of recent logging (Log1, Log2) is minimal (less than 10%). Unit HD3 had the highest rate of forest harvesting in the 1970s (Log1) and 1980s (Log2). Unit HD4 was the most affected by logging prior to 1970, as indicated on maps based on aerial photos dating back to the 1960s. However, some stands harvested during the 1920-1940 period and considered young forests do not appear as logged areas on 1970s maps. Consequently, logging areas are underestimated on the 1970s forest maps. Logging stretched mainly along a series of small forest villages that follow a railway line crossing the unit. Logging and coal-fired steam locomotives were responsible for some human-induced fires (Hf1, Hf2). Unit HD5 is also strongly influenced by human activities, with a long history of logging (Log1, Log2) and numerous human-induced fires (Hf1). The strong effect of human activities in units HD2 and HD5 is reflected in the abundance of human-induced fires that favoured the development of *Populus tremuloides*. Farther north, unit HD6 was logged extensively during the 1980s (Log2). These activities have since moved still further north (HD7).

In order to improve the methodology used in this study, maps of vegetation themes and sets of explanatory variables could have been elaborated using fuzzy clustering (De Cáceres *et al.*, 2010; Borcard *et al.*, 2011; Duff *et al.*, 2013). In the first stages of development, fuzzy classification might enable vegetation patterns to be summarized using the concept of community, while at the same time recognizing that such communities need not be entirely spatially exclusive. Fuzzy methods have been used to represent uncertainty in the delineation of vegetation classes. These methods might show that some ecological districts are intermediate between two geographical units.

3.4 Relations between geographical units of sets of explanatory variables and unique variation of the variation partitioning

Maps of vegetation themes and sets of explanatory variables have also been used to understand the significance of the unique variation (Figure 2B), particularly the unique variation associated to natural disturbances. Appendix 3E compares the natural disturbances, characterized by three distinct sections (south, central, north), and the physical environment. This last set shows a gradual increase or decrease in regard to explanatory variables from the southeastern to the northwestern part of the study area along the latitudinal-oblique gradient.

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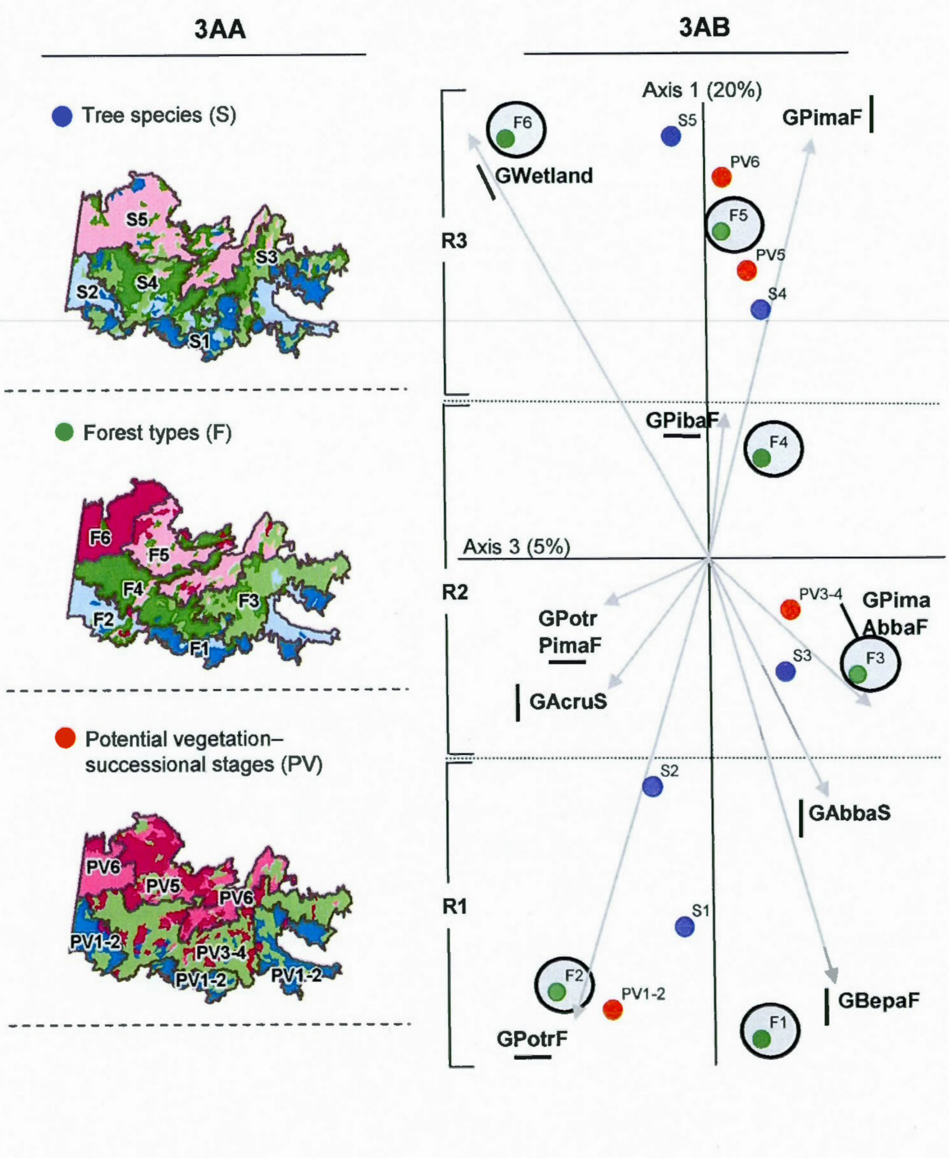
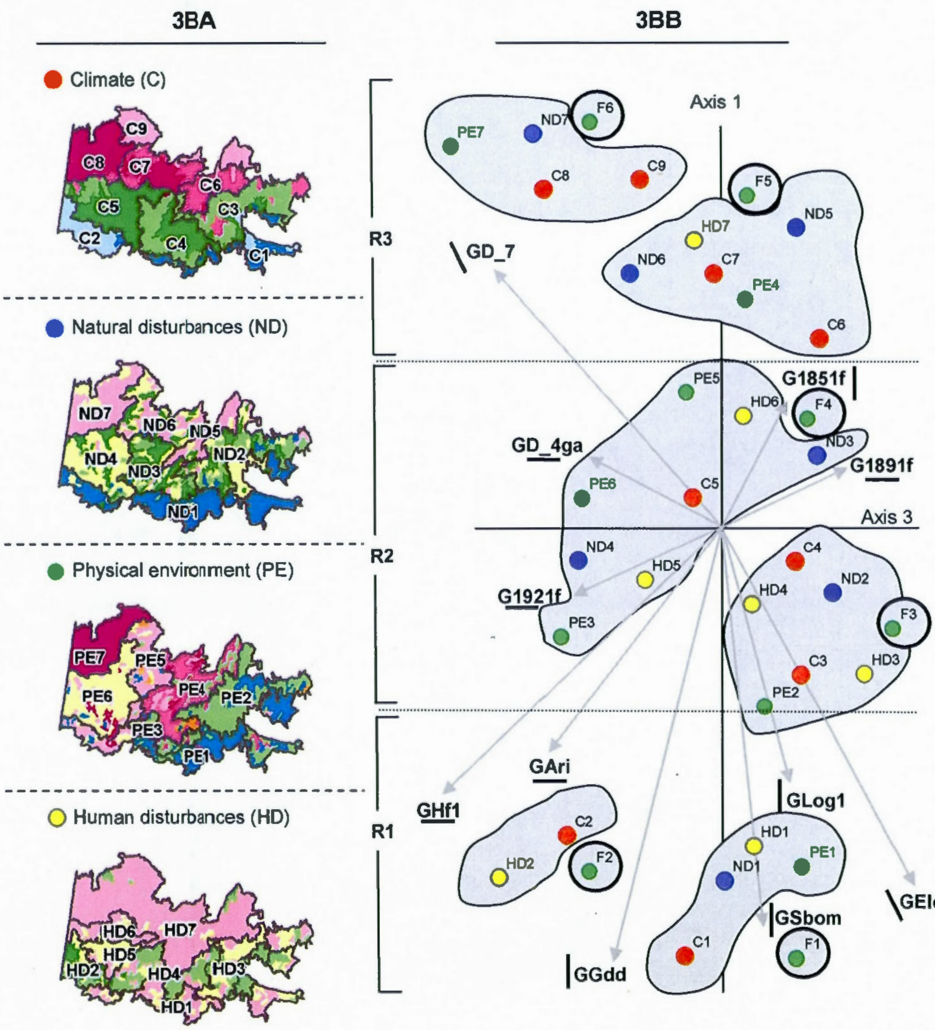
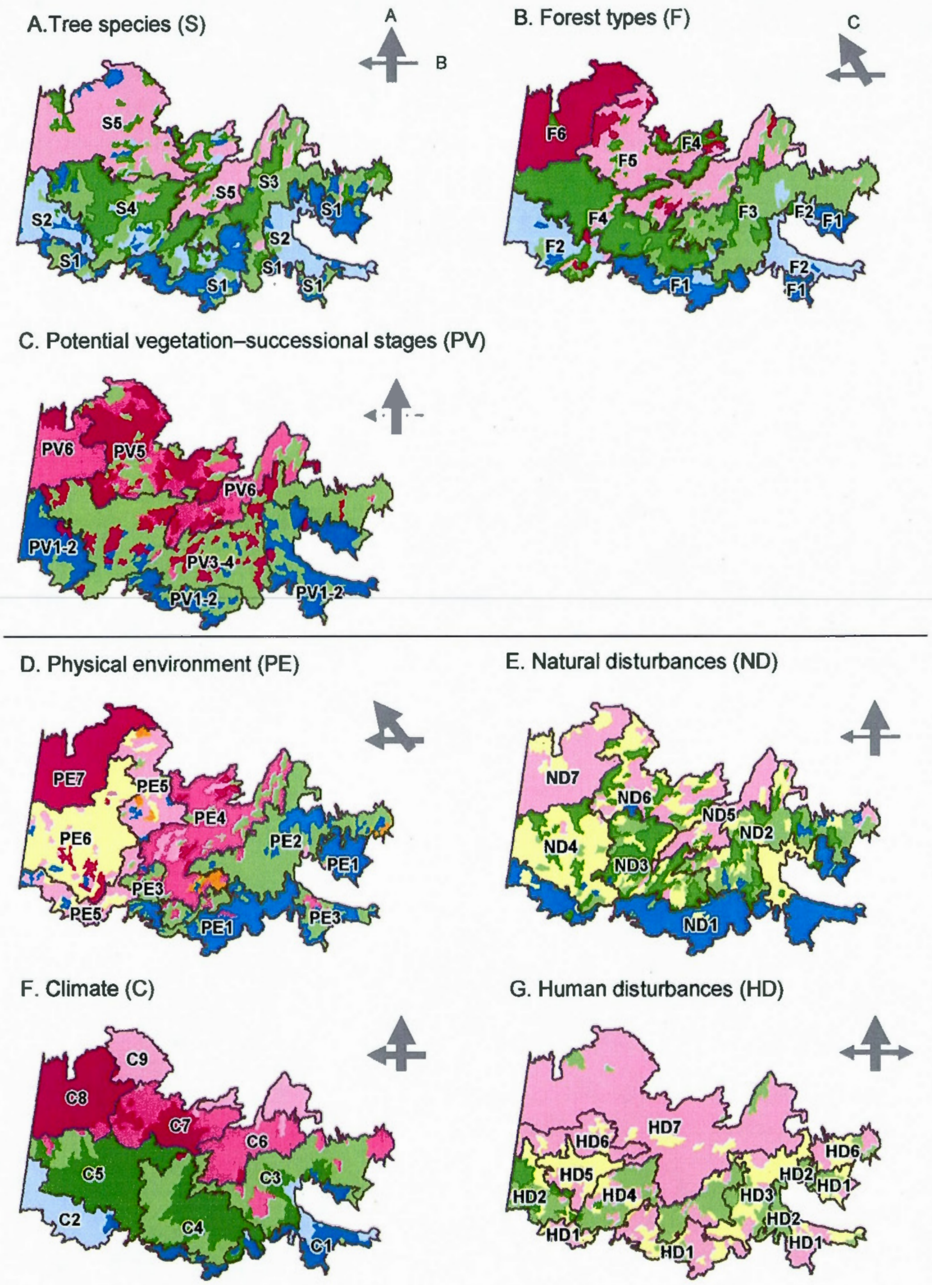
Appendix 3A. Landscape heterogeneity of vegetation themes described by (A) maps (groups of ecological districts and geographical units) and (B) an ordination diagram (groups of vegetation variables (e.g. GPotrF) and geographical units of vegetation themes (e.g. F1)). The ordination is formed by axis 1 and axis 3 of the RDA. Each group of variables is characterized by its ecological gradient as deduced from the distribution of the variables (latitudinal gradient |, latitudinal-oblique gradient \ and longitudinal gradient —). Maps and an ordination diagram are used to define three overlapping regions (R1 to R3). The meanings of groups of variables are presented in Table 1.1. The black circle around F1, F3, and F5 indicates that these geographical units will be highlighted in Appendix 3B to show the overlap between the vegetation theme and sets of explanatory variables. The maps are presented in Appendix 3C.



Appendix 3B. Landscape heterogeneity of sets of explanatory variables described by (A) maps (groups of ecological districts and geographical units) and (B) an ordination diagram (groups of explanatory variables (e.g. GGdd), and geographical units of sets of explanatory variables (e.g. PE1). The ordination is formed by axis 1 and axis 3 of the RDA. Each group of variables is characterized by its ecological gradient as deduced from the distribution of the variables (latitudinal gradient |, latitudinal-oblique gradient \ and longitudinal gradient —). F1: links between geographical unit F1 of the forest type theme and geographical units of several sets of explanatory variables. F2 to F6: the same as F1, with other specific geographical units of sets of explanatory variables. Maps and the ordination diagram are used to define three overlapping regions (R1 to R3). The meanings of groups of variables are presented in Table 1.1. The maps are presented in Appendix 3C.



Appendix 3C. Geographical units of vegetation themes (S: tree species, F: forest types, PV: potential vegetation–successional stages) and sets of explanatory variables (PE: physical environment, C: climate, ND: natural disturbances, HD: human disturbances). An estimate of the ecological gradients is shown near the maps.



Appendix 3D. Description of geographical units of vegetation themes (S: tree species, F: forest types, PV: potential vegetation–successional stages) and sets of explanatory variables (PE: physical environment, C: climate, ND: natural disturbances, HD: human disturbances). The geographical units are delineated in Appendix 3C. The responses variables are defined in Appendix 1A and explanatory variables in Appendix3D.

Tree species

	Hardwood tree species					Coniferous tree species				
Unit	BealS	AcruS	BepaS	PotrS	SaspS	PiglS	PimaS	PibaS	AbbaS	ThocS
S1	1.7	0.6	22.0	6.2	0.3	2.9	29.9	6.4	22.1	0.2
S2	0.7	0.9	15.3	23.3	2.5	2.6	23.3	13.4	10.9	0.5
S3	0.0	0.0	12.3	3.3	0.1	1.1	53.2	8.0	14.9	0.0
S4	0.0	0.1	9.5	6.7	0.5	0.7	53.8	18.2	7.1	0.1
S5	0.0	0.0	3.3	3.3	0.3	0.4	77.3	5.8	5.3	0.1

Forest types

	Hardwood forest types			Mixedwood forest types				Coniferous forest types				Others		
Unit	BepaF	BealF	PotrF	Bepa PimaF	Bepa AbbaF	Potr PimaF	Potr AbbaF	PimaF	Pima AbbaF	PibaF	AbbaF	Alru	Wetland	Heathland
F1	15.6	1.4	3.1	14.4	11.7	3.1	0.6	20.8	2.5	6.2	2.3	1.3	3.3	0.5
F2	6.0	0.5	12.8	7.9	2.4	9.6	2.4	17.6	2.0	8.5	1.7	3.6	7.9	2.4
F3	2.7	0.0	2.0	6.6	3.6	2.5	0.2	31.1	7.0	13.4	5.7	1.0	4.6	1.3
F4	2.1	0.0	2.1	5.4	1.8	5.2	0.4	28.5	1.8	22.3	0.8	1.7	13.5	0.8
F5	0.7	0.0	0.9	3.3	0.4	2.2	0.0	47.5	2.3	8.4	0.6	2.2	12.9	1.4
F6	0.0	0.0	0.1	0.1	0.0	0.6	0.0	27.6	0.4	2.9	0.0	0.9	50.2	1.6

Potential vegetation – successional stages

	Ms2 (Abies – Betula)					Rs2 (Abies – Picea)					Re2 (Picea mariana)				
Unit	Ms2S2	Ms2S3	Ms2S4	Ms2S5	Tot	Rs2S2	Rs2S3	Rs2S4	Rs2S5	Tot	Re2S2	Re2S3	Re2S4	Re2S5	Tot
PV1-2	21.9	9.6	5.6	4.6	41	8.3	6.8	5.9	8.1	29	13.7	1.5	2.3	1.7	17
PV3-4	7.5	3.6	3.3	4.4	18	9.9	6.7	6.7	11.0	34	28.1	4.4	5.5	7.9	38
PV5	2.5	1.0	0.3	0.2	4	9.5	2.8	4.6	7.8	24	36.6	3.4	5.1	21.8	45
PV6	1.2	0.8	0.7	0.9	3	5.8	3.1	3.3	12.3	24	29.8	2.3	4.4	35.2	36

Physical environment

	Physiography						Surficial deposits									Other
Unit	Malt	S_a	S_b	S_c	S_d	Ele	D_1a	D_1ar	D_2a	D_2b	D_4ga	D_4gs	D_7	D_wa	D_r	L_100km²
PE1	454	35	18	24	19	82	32	41	2	8	0	0	1	7	9	1
PE2	414	45	24	17	11	61	47	23	4	9	0	0	3	7	4	1
PE3	431	57	18	18	7	52	49	17	4	12	0	1	5	10	1	1
PE4	401	79	13	6	2	33	46	10	5	5	1	3	14	12	2	1
PE5	314	70	17	9	3	28	19	13	2	0	26	9	14	9	8	1
PE6	300	85	11	3	1	21	5	7	1	0	52	5	19	6	4	0
PE7	242	93	5	1	1	11	2	1	0	0	6	0	63	7	3	1

Natural disturbances

	Spruce budworm outbreaks						Fires					Other
Unit	Sbos	Sbon	Sbom	1921o	1891o	1851o	Fia	Fif	1921f	1891f	1851f	Wi
ND1	2.3	19.4	19.7	26.2	10.5	10.8	4.0	1.3	16.8	10.9	9.3	0.3
ND2	0.3	7.7	4.8	8.5	11.4	12.8	4.5	1.5	20.4	19.7	17.6	0.4
ND3	0.6	5.8	2.9	5.6	6.2	4.3	1.7	0.8	34.0	23.0	19.0	0.9
ND4	0.5	5.3	3.0	10.8	4.4	6.6	3.8	0.6	33.1	15.4	18.3	0.5
ND5	0.2	3.3	0.7	3.0	4.3	9.3	3.3	1.8	21.8	13.5	33.5	1.1
ND6	0.9	3.3	1.6	2.9	3.7	5.6	5.4	1.2	31.0	13.1	30.1	1.6
ND7	0.1	0.5	0.2	0.7	1.3	4.3	6.0	0.9	13.7	10.9	43.1	0.3

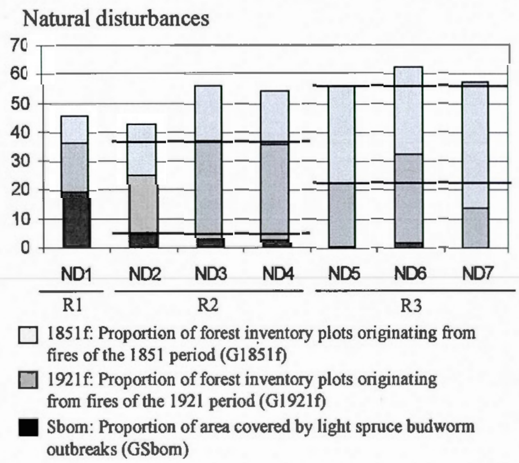
Climate

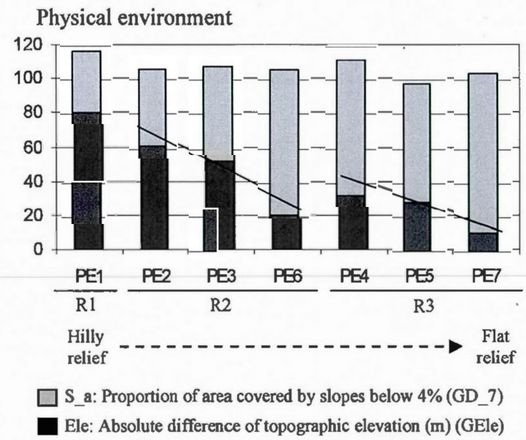
	Aridity regime			Thermal regime				
Unit	Preci	Vpd	Ari	Gdd	Mat	Dwf	Dwfc	Ef
C1	340	1288	1.6	1331	1.2	176	99	248
C2	302	1386	2.1	1349	1.1	175	95	249
C3	331	1232	1.3	1222	0.2	170	94	245
C4	337	1277	1.5	1270	0.5	173	94	247
C5	319	1312	1.6	1258	0.4	173	92	246
C6	332	1195	1.2	1167	-0.6	165	90	242
C7	313	1251	1.4	1166	-0.5	165	86	242
C8	296	1287	1.8	1142	-0.5	165	85	240
C9	309	1165	1.5	1069	-1.4	163	85	241

Human disturbances

	Logging			Fires		Agriculture		
Unit	1951	Log1	Log2	Hf2	Hf1	Fal	Ag1	Ag2
HD1	9.4	14.8	13.8	12.8	6.8	0.2	0.5	0.3
HD2	14.6	7.2	8.4	66.6	38.6	3.6	5.7	4.6
HD3	12.6	26.4	31.3	35.9	3.3	0.0	0.0	0.0
HD4	20.0	7.7	10.5	64.1	6.4	0.2	0.3	0.2
HD5	12.6	17.1	29.5	7.1	12.8	1.4	1.8	1.2
HD6	3.3	5.6	27.0	10.0	2.7	0.0	0.0	0.0
HD7	4.4	0.7	3.9	3.5	0.9	0.0	0.0	0.0

Appendix 3E A substantial proportion of unique variation for natural disturbances in the tree species and potential vegetation-successional stages themes is caused by the independence of natural disturbances from changes in other sets, such as physical environment. For natural disturbances, the proportion of some explanatory variables (e.g., 1921f) is similar in a specific region of overlap (R1 to R3, Appendices 3A, 3B) and from the eastern part of the study area to the western part. For physical environment, the proportion of some explanatory variables decreases (Ele) or increases (S_a) regularly from the south to the north of the study area and from the eastern part to the western part. Geographical units (ND1 to ND7, PE1 to PE7) are plotted on the ordination diagram of Appendices 3A and 3B. Geographical units are also presented on maps in Appendix 3C.





APPENDIX 4

VEGETATION VARIATION PARTITIONING

The vegetation variation partitioning of the explanatory variables corresponds to the third step of this study, the two first being the ecological gradients and the description of the overlap between response and explanatory variables. The variation partitioning follows the six steps proposed by Borcard *et al.* (2011) as adapted to our study: 1) creation of a separate Y-matrix for each vegetation theme (Y-species, Y-forest types, Y-potential vegetation); 2) Hellinger transformation for each Y-matrix; 3) creation of a separate X-matrix for each of the four sets of explanatory variables (X-c, X-nd, X-pe, X-hd); 4) creation of parsimonious X-matrices by running four separate RDA-based forward selections, using an adjusted R^2; 5) variation partitioning of each Y-matrix using the four parsimonious X-matrices; and 6) tests of significance (by permutations) on all 16 testable fractions of variation obtained from the analysis (15 of these define the explained variation, and 11 are common to 2, 3 or 4 sets of explanatory variables, which means that the variables of these sets are correlated). All testable fractions were considered significant.

Appendix 4A provides more information on the composition of the parsiminious X-matrices used in partitioning vegetation variation. These variables are characterized according to their rank as conferred by a step-by-step selection of all variables (Borcard *et al.*, 2011).

- For the set of explanatory variables relating to physical environment, two main variables have an effect on all themes: the absolute difference in topographic elevation (Ele) and the area covered by organic deposits (D_7). These variables are in opposition along the latitudinal-oblique gradient (Appendix 2D).
- Relative to natural disturbances, three explanatory variables have a particularly strong influence: the spruce budworm outbreaks that occurred at the beginning of the last century (in the 1901-1930 period, variable 1921o), the spruce budworm

outbreak at the end of the 19th century (before 1870, variable 1851o) and fires of the 1921 period (1921f). The first variable belongs to group GSbom (Appendix 2D) and is mainly located in the southern portion of the study area. The second variable is included in group GEle and its distribution corresponds to the southern portion of the latitudinal-oblique gradient. The third variable (1921f) occupies the central portion of the study area. It shows a slight dominance in the western portion, compared to the eastern portion. This is the only variable forming the G1921 group.

- The most important climate variables, regardless of the vegetation theme, are annual average temperature (Mat) and vapor pressure deficit (Vpd). The first variable belongs to group Gdd (annual number of growing degree-days). The distribution of these variables is well-adjusted to the latitudinal gradient. The vapor pressure deficit is part of group GAri, which characterizes the longitudinal gradient (Appendix 2D).

- Three variables related to human disturbances are highlighted in the parsimonious matrices: frequency of human-induced fires per 100 km^2 during the 1938-1998 period (Hfl), area covered by logging during the 1970 period (Log1), and relative proportion of forest inventory plots affected by logging (1951). The first variable belongs to group GHfl (Appendix 2D), which is mainly located in the southwestern portion of the study area, with a small extension into the southeastern portion. The last two variables (Hfl, Log1) form part of the same group (Glog1), which characterizes the latitudinal gradient and reflects the human activities that occurred in the southern portion of the study area.

References

Borcard, D., F. Gillet & P. Legendre, 2011. Numerical Ecology with R. Springer, New York, US.

Appendix 4A. Variables forming the parsimonious X matrices developed for each vegetation theme (X-PE.pars, X-ND.pars, X-C.pars, X-ND.pars). The variables are presented in order of importance.

Set	Code	Explanatory variable	Forest species	Forest types	Pot. veg.-suc. stage
Physical environment	Malt	Mean altitude (m)	3	3	8
	Ele	Absolute difference of elevation between upper and lower portion of the landscape (m)	1	1	1
	D_wa	Relative proportion of area covered by water	6		
	D_4ga	Area covered by glaciolacustrine fine-textured (clay) surficial deposit	5	8	
	D_4gs	Area covered by glaciolacustrine coarse-textured (sand) surficial deposit	10	7	5
	D_2a	Area covered by juxtaglacial deposits		12	4
	D_2b	Area covered by proglacial deposits	9	4	6
	D_7	Area covered by organic deposits	2	2	3
	S_a	Area covered by slopes below 4%		11	
	S_b	Area covered by slopes ranging from 4 to 8%		10	
	S_c	Area covered by slopes ranging from 9 to 15%			
	S_d	Area covered by slopes over 15%	8		9
	D_1a	Area covered by thick till (more than 1m)	4	5	2
	D_1ar	Area covered by thin till (less than 1m)	7	9	
	D_r	Area covered by rock		6	10
	L_100km^2	Mean number of lakes per 100 km^2		13	7
Natural disturbances	1851o	Plots originating from spruce budworm outbreak before 1870	4	4	2
	1851f	Plots originating from fires before 1870	7	10	6
	1891o	Plots originating from spruce budworm outbreak between 1870 and 1900	2		3
	1891f	Plots originating from fires between 1870 and 1900	3	11	4
	1921o	Plots originating from spruce budworm outbreak between 1901 and 1930	1	3	1
	1921f	Plots originating from fires between 1901 and 1930	5	5	5
	Fia	Area covered by fires	11	9	8
	Wi	Area covered by windthrow	12	6	9
	Sbom	Area covered by light spruce budworm outbreak	6	2	7
	Sbos	Area covered by severe spruce budworm outbreak	9	7	11
	Fif	Number of fires per 100 km^2 during the period 1938-1998	8	8	10
	Sbon	Number of years of infestation by spruce budworm during the period 1938-1998	10	1	
Climate	Ari	Aridity index	6	3	6
	Gdd	Annual number of growing degree-days	5	4	7
	Vpd	Vapor pressure deficit (total daily deficit (in mbar) from months June to August)	4	2	2
	Ef	Early frost (Julian day corresponding to the first frost)	7	7	5
	Dwfc	Number of consecutive days without freezing	3	8	
	Dwf	Total number of days without freezing		6	3
	Preci	Rainfall during the growing season (mm)	2	5	4
	Mat	Mean annual temperature	1	1	1
Human disturbances	Ag1	Area covered by agriculture during the 1970 period	6	7	
	Ag2	Area covered by agriculture during the 1980 period	7		
	Log1	Area covered by logging during the 1970 period	3	1	2
	Log2	Area covered by logging during the 1980 period		4	
	Hf1	Number of human-induced fires during the 1938-1998 period	1	2	1
	Hf2	Area covered by human-induced fires since 1940	4	5	4
	Fa1	Area covered by fallow farmland	5	6	
	1951	Plots originating mainly from logging after 1930	2	3	3

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CHAPITRE II

A NEW APPROACH TO ECOLOGICAL LAND CLASSIFICATION FOR THE CANADIAN BOREAL FOREST THAT INTEGRATES DISTURBANCES

Pierre Grondin, Sylvie Gauthier, Daniel Borcard, Yves Bergeron et Jean Noël

Publié dans *Landscape Ecology* en 2014

v. 29, no1, pages 1-16.

2.1 Résumé

Les approches traditionnelles de la classification écologique du territoire peuvent être bonifiées par l'intégration, a priori, les données décrivant les perturbations (naturelles et humaines), en plus de la végétation, du climat et de l'environnement physique. Pour développer cette nouvelle approche, nous avons étudié un territoire d'environ 175 000 km^2 dans les domaines bioclimatiques de la sapinière à bouleau blanc et de la pessière noire à mousses de la forêt boréale du Québec, dans l'est du Canada. Des placettes d'inventaire ainsi que des cartes d'inventaire forestiers produites par le ministère des Ressources naturelles du Québec de 1970 à 2000 ont été utilisés pour caractériser 606 districts écologiques (superficie moyenne de 200 km^2) selon trois thèmes de la végétation (espèces forestières, types forestiers et végétations potentielles-stades évolutifs) et quatre ensembles de variables explicatives (climat, environnement physique, perturbations naturelles et humaines). Des analyses de redondance, de groupement (*K*-means) et de partitionnement de la variation de la végétation ont été utilisées pour définir, décrire et comparer les unités homogènes de végétation. La classification du territoire d'étude sur la base des unités homogènes est hiérarchique et composée de trois niveaux d'observation. Parmi les 14 unités homogènes qui composent le niveau le plus détaillé, certaines sont dominées par des forêts relativement jeunes provenant de feux de la période centrée sur 1921. Dans d'autres, les peuplements forestiers sont plus âgés (feux de la période centrée sur 1851), certains sont influencés par les épidémies d'insectes et les incendies (partie sud) tandis que les autres sont fortement affectées par les activités humaines et l'expansion du peuplier faux-tremble. Pour l'ensemble de la zone d'étude et des portions de cette dernière, le partitionnement révèle que les perturbations naturelles est la famille de variables expliquant le mieux la variation spatiale de la végétation. Cependant, la combinaison des perturbations naturelles, du climat, du milieu physique et des perturbations humaines explique toujours une forte proportion de la variation. Notre approche, appelée «classification écologique des unités homogènes de végétation» est plus complète que les classifications précédentes puisqu'elle combine les concepts et les objectifs de l'écologie du paysage et de l'aménagement écosystémique.

Mots clés: Classification écologique du territoire, gradients écologiques, unité homogène de végétation, perturbations naturelles, perturbations humaines, analyse de redondance, groupement *K*-means, partionnement de la variation de la végétation

2.2 Abstract

Traditional approaches to ecological land classification (ELC) can be enhanced by integrating, a priori, data describing disturbances (natural and human), in addition to the usual vegetation, climate, and physical environment data. To develop this new ELC model, we studied an area of about 175,000 km^2 in the *Abies balsamea–Betula papyrifera* and *Picea mariana*-feathermoss bioclimatic domains of the boreal forest of Québec, in eastern Canada. Forest inventory plots and maps produced by the Ministère des Ressources naturelles du Québec from 1970 to 2000 were used to characterize 606 ecological districts (average area 200 km^2) according to three vegetation themes (tree species, forest types, and potential vegetation-successional stages) and four sets of explanatory variables (climate, physical environment, natural and human disturbances). Redundancy, cluster (*K*-means) and variation partitioning analyses were used to delineate, describe, and compare homogeneous landscapes units. The resulting ELC is hierarchical with three levels of observation. Among the 14 homogeneous landscape units composing the most detailed level, some are dominated by relatively young forests originating from fires dating back to the period centered on 1921. In others, forest stands are older (fires from the period centered on 1851), some are under the influence of insect outbreaks and fires (southern part), while the rest are strongly affected by human activities and *Populus tremuloides* expansion. For all the study area and for parts of it, partitioning reveals that natural disturbance is the dominant data set explaining spatial variation in vegetation. However, the combination of natural disturbances, climate, physical environment and human disturbances always explains a high proportion of variation. Our approach, called "ecological land classification of homogeneous landscapes units (ELCH)", is more comprehensive than previous ELCs in that it combines the concepts and goals of both landscape ecology and ecosystem-based management.

Key words: Ecological land classification; Ecological gradients; Homogeneous landscape units; Natural disturbances; Human disturbances; Redundancy analysis; *K*-means clustering; Variation partitioning of vegetation

2.3 Introduction

In natural and human-dominated environments, the interplay between biotic and abiotic forces creates spatial heterogeneity. This heterogeneity generally takes the form of a mosaic composed of patches, each defined by specific relationships between vegetation and environmental conditions (Jenny 1958; Whittaker 1967; White 1979; Urban et al. 1987; Legendre and Fortin 1989; Wu and Loucks 1995; Grossman et al. 1999; Wagner and Fortin 2005). The patches, as represented on a forest map delimiting numerous stands, can be analyzed to define the ecological forces (e.g., latitudinal gradient) structuring the heterogeneity of an area (Hills 1960; Damman 1979; Zonneveld 1989; Gerardin and Ducruc 1990). Patches can be positioned on an ordination diagram along ecological gradients (continuum concept) and then grouped to form homogeneous landscape units (community concept) (Whittaker 1967; Ahti et al. 1968; Rowe and Sheard 1981; Zonneveld 1989; Borcard and Legendre 1994; McGarrigal and Cushman 2005). A homogeneous landscape unit is a portion of land with specific vegetation, physical environment, climate, and disturbance characteristics (both natural and human) (Rowe 1962; Daubenmire 1968; Dufrêne and Legendre 1991). From the macro to the micro scale, a hierarchy of increasingly homogeneous landscape units can be defined (Bailey 1987; Urban et al. 1987; Allen and Hoekstra 1992; Klijn and Udo de Haes 1994; White and Jentsch 2001). At the macro scale, climate is the main driver explaining vegetation distribution (Damman 1979; Bailey 1983; Pojar et al. 1987; Allen and Hoekstra 1992; Payette 1992; Bailey 2009). Bioclimatic zones are at this level (Halliday 1937; Hare 1950; Saucier et al. 2009). At the meso scale, climate, physical features, and disturbances are considered. Finally, at the micro scale, the scale of a field observer, microclimate, physical environment, and disturbances are important variables (Bailey 1987; Lertzman and Fall 1998).

Understanding the causes of spatial heterogeneity and how they vary with scale is a central theme in landscape ecology (Turner 1989; Turner et al. 1993; White et al. 1999). Statistical methods have been developed to test hypotheses about landscape diversity (Borcard et al. 1992; Legendre et al. 2005; Peres-Neto et al. 2006; Tuomisto and Ruokolainen 2006). Ecological land classification (ELC), a field related to landscape and numerical ecology, aims to divide large territories into relatively homogeneous landscape units at different levels of observation, and to characterize the contribution of various sets of explanatory variables to vegetation variation. Knowledge of these patterns and processes, and the ecological gradients creating them, is important for ecosystem-based management and biodiversity conservation (Bailey 1983; Gauthier et al. 2001; Legendre et al. 2005; Bailey 2009). Historically, ELC has adopted two main approaches.

The first approach is based on vegetation–climate relationships and the second on relationships between vegetation, climate, and the physical environment (Bailey et al. 1985). The first approach was mainly used from the beginning of the twentieth century to the 1970s. The aim was to identify vegetation changes on mesic soils along ecological gradients (latitudinal, longitudinal, altitudinal) and to associate these changes to macroclimatic variations (temperature and precipitation). Changes in regional (or zonal) vegetation and climate along gradients justified the delineation of bioclimatic units on a subcontinental scale (Halliday 1937; Hustich 1949; Hare 1950; Dansereau 1957; Rey 1960; Küchler 1964; Grandtner 1966; Ahti et al. 1968; Rowe 1972).

The second approach evolved with the influence of geomorphology and a desire to understand ecosystem relationships at a finer scale to help guide resource management decision making. Using ground plots, aerial photographs and satellite images, the physical environment (edaphic-topographic criteria) and its relationship with vegetation and climate were analyzed to delineate biogeoclimatic units. These studies generally covered smaller areas (meso scale) than the vegetation-climate approach (macro scale). From this perspective, within homogeneous ecological units, similar site conditions are expected to support the same type of plant community, including the assemblage of tree species. Together, *Betula papyrifera*, *Populus tremuloides*, *Abies balsamea*, and *Picea glauca* constitute an example of an assemblage existing on sites with specific combinations of physical features, microclimate, and disturbances. The early-successional stage is dominated by the light-demanding species (e.g., *B. papyrifera*) of this assemblage, which are progressively replaced in late-successional stages by shade tolerant species (e.g., *A. balsamea*), as time since the last disturbance increases. Landscapes with high fire frequencies (e.g., <150 years) are characterized by a large proportion of area occupied by early-successional species (Bergeron et al. 2001; Gauthier et al. 2001; Couillard et al. 2012). This description of forest dynamics corresponds to the notions of potential vegetation (Küchler 1964; Powell 2000; Saucier et al. 2009), habitat type (Daubenmire 1968), site type (Hills 1960; Pojar et al. 1987), and série de végétation (vegetation series) (Rey 1960; Grandtner 1966). Landscapes can be viewed as a continuum of potential vegetation assemblages along a site gradient (toposequence). Climate–site–vegetation relationships, climatic and edaphic climaxes, site potential and toposequence are key words within this second approach. (Hills 1960; Rowe 1962; Whittaker 1967; Jurdant et al. 1977; Bailey 1983, 2009). The concept of permanence comes into play in this approach, which doesn't explicitly deal with disturbances.

Although they had received some attention since the beginning of the twentieth century (Clements 1910), natural disturbances have been studied more intensively since 1970 (Heinselman 1973; Payette 1992; Turner et al. 1993; Bergeron et al.

2001). Emphasis has been placed on characterizing the spatial and temporal variability of disturbance regimes (e.g., fire frequency). These studies have demonstrated that forest landscapes are more complex and diversified than originally estimated. Dynamic equilibrium, landscape heterogeneity, and hierarchical patch dynamics are the main concepts structuring these analyses (White 1979; McCune and Allen 1985; Wu and Loucks 1995; Cleland et al. 1997; White et al. 1999; Powell 2000). ELCs were adapted to acknowledge this new approach, which assumes that vegetation is controlled mainly by climate and natural disturbances (Omi et al. 1979; Cissel et al. 1999). From this perspective emerged a landscape classification based on natural disturbance characteristics (fire) in connection with more or less stable vegetation (equilibrium). This approach was mostly applied to larger vegetation landscapes, but could also be considered at a finer scale to the dynamics of a site (Turner et al. 1993; Lertzman and Fall 1998; White et al. 1999). More recently, human-caused disturbances have been identified as an important driver of landscape dynamics. Anthropogenic activities have altered landscape age class distribution by provoking the loss of old forests (Boucher et al. 2009; Cyr et al. 2009), and have homogenized forest composition by substantially increasing the frequency of early-successional stands on various sites along the toposequence. The relationship between vegetation and the physical environment then becomes much more diffuse than in natural environments (Carleton and MacLellan 1994; Östlund et al. 1997; Lorimer 2001; Schulte et al. 2007; Laquerre et al. 2009). However, ELCs have not yet incorporated human disturbances and are therefore missing an important driver of landscape change (Ohmann and Spies 1998).

The first goal of this research is to classify the heterogeneity of the study area within a hierarchy of relatively homogeneous landscape units, on the basis of vegetation and four sets of explanatory variables (climate, physical environment, natural and human disturbances). The second goal is to quantify the proportion of vegetation variation explained by each set and their combinations for some levels of observation in the hierarchical classification.

2.4 Methods

2.4.1 Study area

The study region (175,000 km^2) belongs to the circumboreal zone, and forms an important part of two bioclimatic domains: the *A. balsamea*–*B. papyrifera* in the south, and further north, the *Picea mariana*-feathermoss domain (Rowe 1972; Saucier et al. 2009) (Fig. 1). Six of the boreal zone's most common tree species are well represented. Three are shade-tolerant species: *Picea mariana* (Mill.) BSP., *A. balsamea* (L.) Mill., and *Picea glauca* (Moench) Voss. Three are light-demanding species: *Pinus banksiana* Lamb., *B. papyrifera* Marsh., and *P. tremuloides* Michx. The proportions of these species change along ecological gradients describing the climate, physical environment, and natural and human disturbances. These gradients are used to define and describe homogeneous landscape units. Human disturbances are included in the explanatory variables because some portions of the study area have been affected by anthropogenic activities for almost 100 years.

2.4.2 Sources of information

This study draws on two main contemporary sources of information: forest inventory plots (n=53 635) and geospatial databases derived from forest maps. These databases have been developed from Spatial Information on Forest composition based on Tessera (SIFORT). Forest maps from 1970 to 1980 make up the SIFORT-1 database, and forest maps from 1980 to 1990, the SIFORT-2 database. These information sources have been used to characterize 606 ecological districts. The average area of the districts is 200 km^2. Each ecological district corresponds to a uniform area described by a specific pattern of surficial deposits, topography, and regional vegetation (Robitaille and Saucier 1998), and was characterized by vegetation (Y-matrix) and explanatory variables (X-matrix).

The Y-matrix was constructed using three complementary vegetation themes, each corresponding to a different aspect or organization level of the vegetation: tree species (e.g., the abundance of *Pinus banksiana* as a species in an ecological district), forest types (e.g., the abundance of forest stands dominated by *Pinus banksiana*), and the combination of potential vegetation types and successional stages (e.g., Re2-S2: *Picea mariana* potential vegetation-Re2 in the early stage of succession-S2) (Appendix 1). The description of tree species and potential vegetation-successional stages is based on forest inventory plots (1970–2000). The SIFORT-2 database was used to describe the forest types.

The X-matrix contains the description of the 606 ecological districts in relation to four sets of explanatory variables (Appendix 2). Climatic variables were estimated using data recorded at meteorological stations and extrapolated to each ecological district by the BioSIM simulator (Régnière 1996). The physical environment was characterized according to the Ministère des ressources naturelles du Québec (MRN) database describing each ecological district, including the relative proportion of area for each surficial deposit type and physiographic variable (Robitaille and Saucier 1998). Natural disturbances were described in terms of the recent history of fires, insect outbreaks, and windthrows over the last 100–150 years. Forest maps (SIFORT-2) were used to evaluate the areas affected by light and severe epidemics, windthrows, and fires. Forest inventory plots were used to characterize fire history relative to periods of origin (e.g., 1901–1930). In this article, each of these periods is named according to a year close to its central year (e.g., the 1901–1930 period is referred to as the period centered on 1921). The number of years of infestation by spruce budworm and the frequency of natural fires per 100 km^2 from 1938 to 1998 were derived from MRN archives. Human disturbances were described by the relative proportions of agriculture, fallow land, logging, and human-induced fires (from 1938 to 1998). These variables were obtained from forest maps (SIFORT-1 and 2).

2.4.3 Data analysis (Fig. 2.2)

2.4.3.1 Unconstrained analysis

An unconstrained analysis involving vegetation alone was run to illustrate ELCs produced by pioneers in this field (Halliday 1937; Dansereau 1957; Küchler 1964; Rowe 1972). This analysis was performed using the R statistical language (R Development Core Team, 2010). A *K*-means clustering of the 606 districts was computed for the three vegetation themes (Legendre and Legendre 2012). Prior to clustering, the variables were subjected to a Hellinger transformation to give less weight to abundant tree species and preserve an ecologically meaningful distance among sites (Legendre and Gallagher 2001).

2.4.3.2 Constrained analysis, delineation of homogeneous landscape units, and variation partitioning of the vegetation

The ecological land classification of homogeneous landscape units (ELCH) was developed using a redundancy analysis (RDA) involving a Y-matrix formed by all vegetation themes (tree species, forest types, potential vegetation-successional stages) and constrained by an X-matrix composed of four sets of explanatory variables (climate, natural disturbances, physical environment, and human disturbances). All canonical axes resulting from the RDA were submitted to *K*-means clustering in order to form groups of ecological districts. *K*-means clustering allows the formation of two or more groups of ecological districts. While *K*-means results can be completely hierarchical (smaller groups nested in larger ones), the method does not guarantee this outcome (Legendre and Legendre 2012). This gradual stratification was used to develop a hierarchy of homogeneous landscape units formed of three levels of observation. The landscapes were positioned on an ordination diagram according to the centroid of each landscape, as calculated using the canonical scores of each ecological district. Ordination axis 1 was positioned vertically and axis 2 horizontally, because this configuration represents north–south and east–west gradients in their usual orientation in the study area. The homogeneous landscape units were also characterized using histograms showing the relative proportions of period of origin and disturbance type (fires or insect outbreaks) noted in each forest inventory plot. Variation partitioning of the vegetation was used to quantify the contribution of each set of explanatory variables to vegetation changes along the levels of observation considered in this study (Borcard et al. 1992; Legendre et al. 2005; Peres-Neto et al. 2006; Tuomisto and Ruokolainen 2006). Variation partitioning was performed following the steps proposed by Borcard et al. (2011).

2.5 Results

An overview of the vegetation of the study area is used as an introduction to the ELCH. Other descriptions in line with approaches presented in the introduction are described in Appendix 3.

2.5.1 The vegetation of the study area

Nine classes of vegetation, combining dominant tree species, forest types, and potential vegetation-successional stages, describe the vegetation of the area. The following description is restricted to tree species because this theme provides a good overview of the vegetation heterogeneity (Fig. 2.3). Eastern units V-1, V-2, and V-3 are characterized by an abundance of *Abies balsamea*, *B. papyrifera*, and *Picea mariana*. Towards the north (V-2, V-3), *Picea mariana* becomes more abundant than *Abies balsamea* and *Betula papyrifera*. In the central-eastern unit (V-3), early-successional species (*Populus tremuloides* and *Pinus banksiana*) are abundant. In the north-east, V-4 is dominated by *Picea mariana* and *Abies balsamea*, the latter mainly confined to hills. *Pinus banksiana* is scattered and concentrated on sandy deposits. In the central unit (V-5), *Picea mariana* and *Pinus banksiana* are abundant. A composition similar to V-3 is found in the southern and central-western units (V-6 and V-7), but *A. balsamea* is less abundant than in the east (V-1, V-2, V-3). In the north-west, V-8 shows similarities to V-4 in terms of abundance of *Picea mariana*. Finally, the most northwestern unit V-9 consists mainly of non-forested peatlands and *Picea mariana* on organic deposits.

2.5.2 Ecological land classification of homogeneous landscapes units (ELCH)

2.5.2.1 RDA and mapping of the scores of the first four canonical axes of ecological districts

The ELCH is based on a RDA, and mainly on scores of the first 4 canonical axes. These canonical axes are closely related to ecological gradients describing the heterogeneity of the study area (Fig. 2.2). These first 4 canonical axes of the RDA explain 37 % of the vegetation's variability. The first canonical axis (Fig. 2.4a) reflects the changes in vegetation and explanatory variables occurring from south to north in the study area. For example, changes along the latitudinal gradient are primarily related to the decrease in the annual number of growing degree-days and forest stands affected by the last spruce budworm outbreak (Sbom) (Fig. 2.5a). The second canonical axis (Fig. 2.4b) is described by three longitudinal bands mostly reflecting natural disturbances (Fig. 2.5b). The central band is dominated by relatively young stands (1921f). It differs, on one hand, from the southern portion, which is well populated with *A. balsamea* (AbbaS) whose dynamics are related to Sbom and, on the other hand, from the northern part, where old stands (PimaF, Pima-AbbaF) from fires of the period centered on 1851 (before 1870) are well represented. In the central band, the abundance of sandy deposits favors the presence of young forests often dominated by *Pinus banksiana.*

The third canonical axis (Fig. 2.4c) characterizes changes that occur from south-east to north-west. This latitudinal-oblique gradient is strongly linked to changes in the physical environment (Ele variable, Fig. 2.5c), particularly the transition from a hilly (south-east) to relatively flat topography (north-west). These changes are accompanied by an increase in wetlands (D_7). The fourth canonical axis (Fig. 2.4d) primarily defines the impact of human activities (Fig. 2.5d). From approximately 1880 to 1940, land clearing for agricultural settlement had a widespread impact on both the southeastern and southwestern sectors. Beginning in 1905, coal-fired steam locomotives were used in the southern part of the territory to link the agroforestry regions of Abitibi and Lac Saint-Jean (Fig. 2.1). These activities contributed to numerous human-induced fires (Hfl, Fig. 2.5, Hardy and Seguin 1984) and promoted changes in both age structure and forest composition. These changes consist mostly in the expansion of *P. tremuloides* (PotrF) and the presence of many stands originating from the period centered on 1951 (after 1930). During the second half of the twentieth century, mechanized logging spread throughout the *A. balsamea– B. papyrifera* domain, and gradually towards the north into the *Picea mariana*–feathermoss domain.

2.5.2.2 *K*-means cluster analysis and grouping of ecological districts

A *K*-means clustering applied to the scores of the canonical axes relative to the ecological districts (Fig. 2.2) allows the formation of three groupings of ecological districts (Fig. 2.6). In the first grouping (Fig. 2.6a), ecological districts strongly associated with the *A. balsamea–B. papyrifera* domain are distinguished from those belonging to the *Picea mariana*-feathermoss domain. In the second grouping (Fig. 2.6b), the *Picea mariana*-feathermoss domain is split to highlight the wide central band described by the RDA (Figs. 2.4, 2.5). In the third grouping (Fig. 2.6c), the northern part of this last domain (pink) is characterized according to the proportion of wetlands and related attributes (group 5 vs. group 6). The central band (green, Fig. 2.6b) is divided into an eastern (group 3, Fig. 2.6c) and a western subsection (group 4). *A. balsamea* is more abundant and relief is well defined (hilly) in the eastern subsection (Fig. 2.5). The southern portion (blue) is described relative to the effects of Sboms (group 1, table 2.2) and human disturbances (group 2).

2.5.2.3 Ecological land classification of homogeneous landscapes units (ELCH)

The development of the ELCH is based on ecological gradients described in the two previous sections. The sequence of analyses highlights four results of particular importance in the delineation and description of the ELCH: the third grouping of ecological districts (Fig. 2.6c), the delineation of the homogeneous landscape units (Fig. 2.7a), the ordination diagram showing the position of homogeneous landscape units along ecological gradients (Fig. 2.7c), and the period-disturbance histograms (Fig. 2.7c). The ELCH is hierarchical with three levels of observation (Fig. 2.7). The first level (n = 2, Figs. 2.7b, c) is the most general and highlights the major territory subdivisions corresponding to bioclimatic domains. The second level (n = 4) distinguishes homogeneous landscape units characterizing the southern and the northern portions of the two bioclimatic domains. The third level is composed of nine elements of landscape classification and 14 geographically distinct homogeneous landscape units. Some of the 14 landscapes are dominated by young forests originating from fires dating back to the period centered on 1921 (222, 221, 24, 131). In others, located in the northern part, forest landscapes are older (period centered on 1851: 132, 231, 232, 25). In the southern part, landscapes are under the influence of insect outbreaks and fires (121, 123). In the two southern extremities, landscapes are strongly affected by human activities (21-pe, 14-pe, 11-pe, 122-pe) and *P. tremuloides* expansion (Fig. 2.7; Table 2.1, Appendices 4 to 7). Homogeneous landscape unit 122-pe was not classified as a managed landscape by the numerical analysis (Figs. 2.7A, 2.6C, dark blue-color). Considering the importance of the human activities, we decided to classify this landscape with those affected by human activities (Table 2.1; Fig. 2.5D). The transition from 9 to 14 landscapes of level III is mainly justified by disjunctions in geographic distribution (Fig. 2.7A, 2.7B). For example, landscape 12 is divided into three landscapes 121, 122-pe, and 123 (pe: *Populus* expansion), each occupying a specific portion of the study area. Some landscapes are also distinguished in reference to the geographical units delineated on Fig. 2.6a and b. For example, landscapes 131 and 132 (Fig. 2.7A), which forms a large unit in Fig. 2.6C (pale green), is separated into two landscapes in Fig. 2.6A and b. Landscape 131 is placed high along axis 1 of the ordination diagram (Fig. 2.7C), revealing its affinities with the *Picea mariana*-feathermoss domain. Considering the hilly topography, the relative abundance of *A. balsamea* and its grouping with homogeneous landscape unit 132 in some analyses (Fig. 2.3), we classified homogeneous landscape unit 131 within the northern portion of the *A. balsamea–B. papyrifera* domain.

2.5.2.4 Proportion of variation explained by sets of variables along spatial levels of observation (variation partitioning of vegetation)

After presenting the ELCH, we are now interested in quantifying the relative importance of the four sets of explanatory variables in explaining the vegetation heterogeneity. To achieve this goal, we used the partitioning of vegetation throughout the study area as well as in three portions of it (Fig. 2.8, appendix 8). The analyses reveal that the explained vegetation variation is always greater than the unexplained portion. This suggests that the heterogeneity of the study area, its landscape diversity, is structured along ecological gradients (Legendre et al. 2005). This structure indicates that portions of the territory are different from others, allowing the delineation of homogeneous landscape units.

The total proportion of variation attributed to natural disturbances is relatively high, regardless of geographical entity (Fig. 2.8, NDt). The unique fractions of variation (e.g., NDu) explained by each set of explanatory variables are generally small, except for natural disturbances. This indicates that some changes in natural disturbances are relatively independent of changes in other sets, especially physical environment. The three large latitudinal bands presented previously (southern, central, northern) and characterizing the natural disturbances are the main examples (Figs. 2.4b, 2.6b).

The common fractions of variation explained by the sets of explanatory variables are generally high, especially for natural disturbances (NDc, Fig. 2.8). The common variation of natural disturbances is mainly attributed to triple and quadruple combinations. This result confirms that changes in vegetation are closely related to changes in natural disturbances, in combination with other sets. The total variation explained by climate (Ct) is higher for the entire area than the two bioclimatic domains. The impact of human disturbances (HDt) is generally low, except in the western portion (mainly the Abitibi region), where a high proportion of variation is explained by this set of variables, in combination with the three others (quadruple combination). This indicates that changes in vegetation are closely integrated or dependent on changes in all of the sets, from southern to northern Abitibi (Fig. 2.3, Appendix 7).

2.6 Discussion

2.6.1 The ecological land classification of homogeneous landscapes units (ELCH) supplements ELCs based solely on vegetation

The ELCH is strongly influenced by the pioneers and others authors interested by landscape ecology (e.g., Rowe 1972). The similarity between the vegetation map of the study area (Fig. 2.3) and that of the homogeneous landscape units (Fig. 2.7) reveals that vegetation alone is a faithful indicator, a phytometer, of explanatory variables at the meso scale (Halliday 1937; Hills 1960; Damman 1964; Barnes et al. 1982). However, the ELCH better describes landscapes patterns than ELCs based on vegetation and climate (e.g., Halliday 1937) or using vegetation, climate, and the physical environment (e.g., Hills 1960) (Fig. 2.9).

2.6.2 The ELCH considers natural disturbances and other sets of natural explanatory variables

The usefulness of the ELCH lies in its a priori inclusion of natural disturbances and other natural sets of explanatory variables (climate, physical environment). We have shown that natural disturbances are the predominant set explaining vegetation variation (the sum of unique and common variations). The unique variation explained by natural disturbances is considered to be part of the total variation independent of the other sets of explanatory variables. This unique variation might also be defined as the expression of the dominance of natural disturbances over the other sets. This concurs with authors who consider natural disturbances as overlaying other environmental gradients (Heinselman 1973; White 1987; Payette 1992). In addition, this study has shown that natural disturbances vary regionally (White 1987; Mansuy et al. 2010). Some homogeneous landscape units are dominated by young forests, others are older, some are under the influence of insect outbreaks and fires, while the rest are strongly affected by human activities. These landscape types (younger vs. older), based on natural disturbances criteria, are described by specific age class distributions and are in line with those proposed by Turner et al. (1993) and discussed by Lertzman and Fall (1998) and White et al. (1999). Using the vocabulary of these authors, some landscapes of the study area are more stable than others, or are closer to their equilibrium stage.

Although natural disturbances are the main factor, the variation in vegetation explained by this set in combination with others is larger than the unique variation. Consequently, the control of the vegetation by environmental variables is mainly related to the integration of several sets. This paradigm of multiple factors controlling landscape heterogeneity follows numerous authors (Jenny 1958; White 1979, 1987), including those interested by vegetation variation partitioning (Borcard et al. 1992 and following). The integration of multiple factors is maintained for the entire territory and parts of it, all considered at the meso scale (Damman 1979; Bailey 1987; Lertzman and Fall 1998). At this scale, climate is never the dominant set of variables (Ohmann and Spies 1998). We attribute this result to small changes in temperature and precipitation along the latitudinal gradient of the study area. Two bioclimatic domains are present but the same six main species are still present in the landscapes. Climate rather becomes the main driver of landscape heterogeneity in larger territories (macro scale), such as bioclimatic zones (Damman 1979; Bailey 1983; Allen and Hoekstra 1992; Payette 1992; Wu and Loucks 1995; Grondin et al. 2007).

2.6.3 The ELCH considers human disturbances

The ELCH is also novel by its a priori inclusion of human disturbances. We have demonstrated that human activities do not play a major role in explaining the vegetation variation when the entire territory is considered. However, in the southern two ends which are closest to human settlement, four homogeneous landscape units show a strong anthropogenic influence. These four landscapes are well integrated into the sequence of canonical axes formed by the RDA (Fig. 2.2) and take their place after the sets of natural variables (Figs. 2.4d, 2.6c). These results concur with authors who consider human disturbances as an important factor in natural landscapes transformation, and one of the major issues in the context of ecosystem-based management implementation (Urban et al. 1987; White and Mladenoff 1994; Schulte et al. 2007; Boucher et al. 2009). In Abitibi (western portion of the study area), where human activities have had the greatest impact, two homogeneous landscape units (21-pe and 221) are superimposed on a uniform area with respect to the physical environment (mesic clay deposit), climate, and natural disturbances (abundance of fires centered on the period 1921). This indicates that anthropogenic disturbances can generate specific homogeneous landscape units. On mesic clay deposits, the expansion of *P. tremuloides* and also *A. balsamea* could eventually continue northward, under the influence of logging, to the northern natural limit of *P. tremuloides* (Fig. 2.5d). The abundance of these two species and the consistent decrease of *Picea mariana* in mixed stands of the *Picea mariana*-feathermoss domain, favoured by intensive management practices and, possibly, climatic change, could contribute to the northward expansion of the *A. balsamea–B. papyrifera* domain into the northern boreal forest currently dominated by *Picea mariana* (Grondin and Cimon 2003; Laquerre et al. 2009; Arbour and Bergeron 2011).

2.7 Conclusion

This study builds on the research of authors who have described ecological gradients and used them to define an ELC. Our approach, the ELCH, is original in including, a priori, landscape disturbance patterns (natural and human) as sets of variables. A sequence of numerical analyses (RDA, *K*-means clustering, variation partitioning) has been used to describe the ecological gradients and define an ELC. We have shown that it is possible to elaborate on an ELC by integrating the main factors structuring landscape heterogeneity, even in areas with great variability of natural disturbances and a strong local influence of human disturbances. Landscape spatial heterogeneity of the study area, considered at the meso scale, is mainly explained by natural disturbances in synchronicity and overlapping with changes in the physical environment, climate, and human activities. Our integrative and quantitative approach of ecological gradients enhance and perhaps slightly modifies our perception and understanding of factors causing landscape heterogeneity in the circumboreal forest zone. This study could not have been carried out without the large databases available at the MRN. More detailed data, especially with respect to natural disturbances (fire origin maps), could lead to slightly different and more accurate results. Other numerical analyses could also be tried (e.g., fuzzy clustering). This first ELCH should be considered as a point of reference to define and compare natural and managed landscapes, to initiate more detailed studies on forest dynamics (e.g., natural variability of homogeneous landscape units), and to estimate the effects of climate changes on vegetation.

Acknowledgments Data (plots, maps, archives) used in this study were collected by the staff of the Ministère des ressources naturelles du Québec (MRN) between 1970 and 2000. This study could not have been produced without the effort of many individuals. Comments by Yan Boucher, David T. Cleland, Paul Jasinski, Jason Laflamme, Del Meidinger, Germain Mercier, 2 anonymous reviewers, as well as stylistic revisions by Debra Christiansen-Stowe, Karen Grislis, and Denise Tousignant were all greatly appreciated. We would also like to thank Denis Hotte and Véronique Poirier for their assistance in data analysis and geomatics. This study was funded by the MRN.

Figure 2.1 Location of the study area (outlined in red) according to the ecological land classification of the Ministère des ressources naturelles du Québec (Saucier et al. 2009)

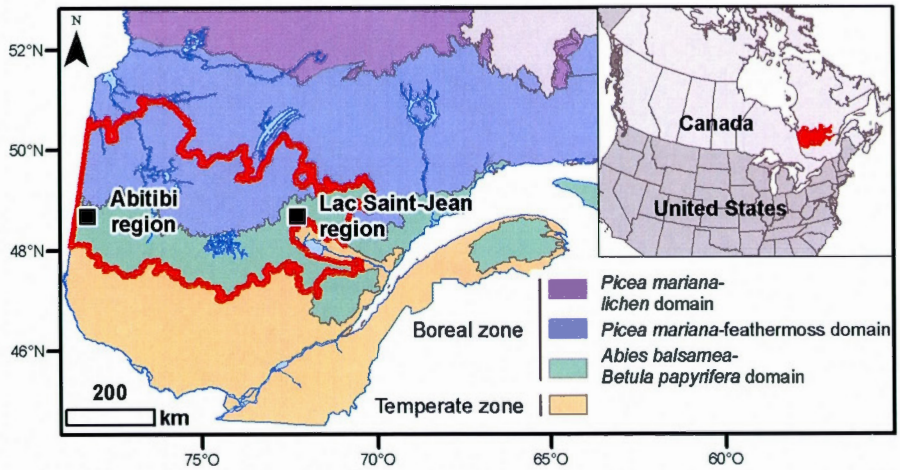


Figure 2.2 Method used A) to define the ecological land classification of homogeneous landscapes units (ELCH) and B) to quantify the proportion of vegetation variation explained by each set of explanatory variables and by their combinations

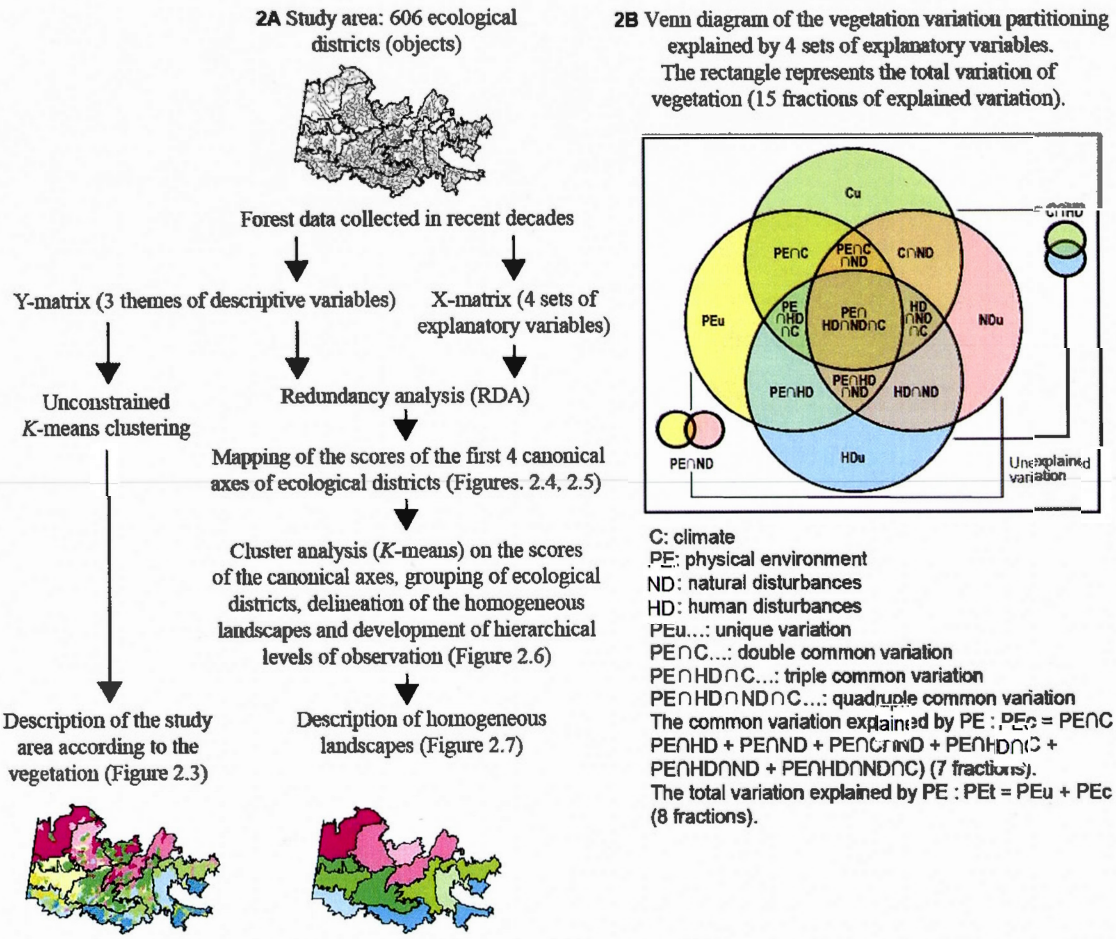
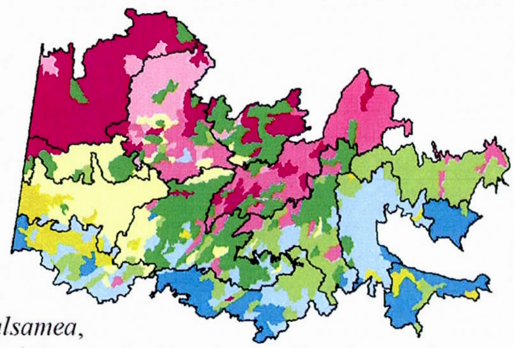


Figure 2.3 Description of the study area according to vegetation (V). The homogeneous landscape units defined in Fig. 2.7A are outlined in black.



*Dominant tree species: Abba: *Abies balsamea*, Bepa: *Betula papyrifera*, Piba: *Pinus banksiana*, Pima: *Picea mariana*, Potr: *Populus tremuloides*, Wetland: non forested peatlands

Figure 2.4 Maps of the scores of the first 4 canonical axes of the ecological districts of the redundancy analysis (RDA, Fig. 2.2). The darker the red, the higher the positive scores. The variation explained by each canonical axis is indicated in brackets. The homogeneous landscape units defined in Fig. 2.7A are outlined in black

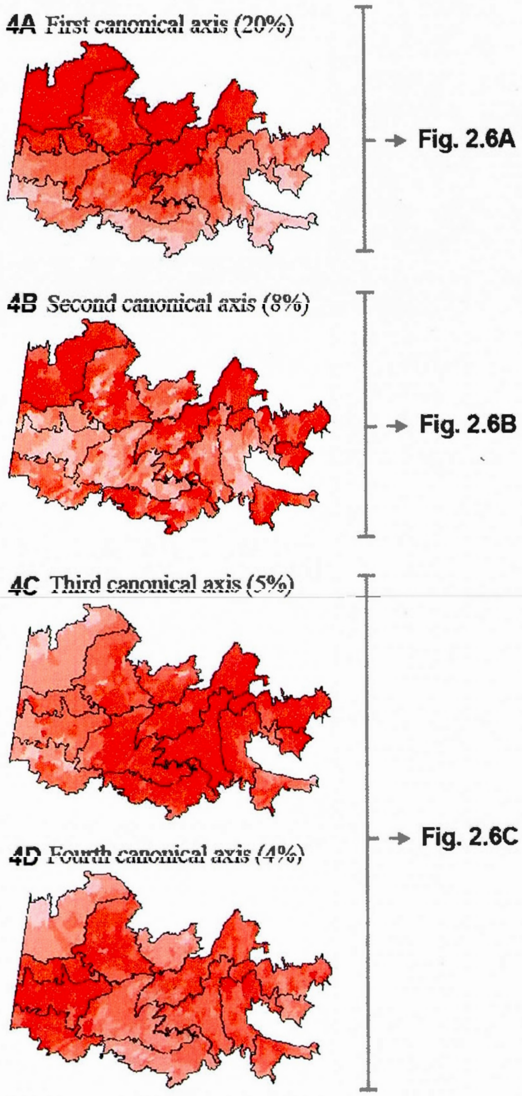


Figure 2.5 Vegetation and explanatory variables related to the first 4 canonical axes of the redundancy analysis (RDA, Fig. 2.2). A) Variables with the highest positive scores on the canonical axis. B) Variables with the highest negative scores on the canonical axis. Codes and description of variables are presented in Table 2.2. On the maps, the darker the gray, the greater the proportion of the variable

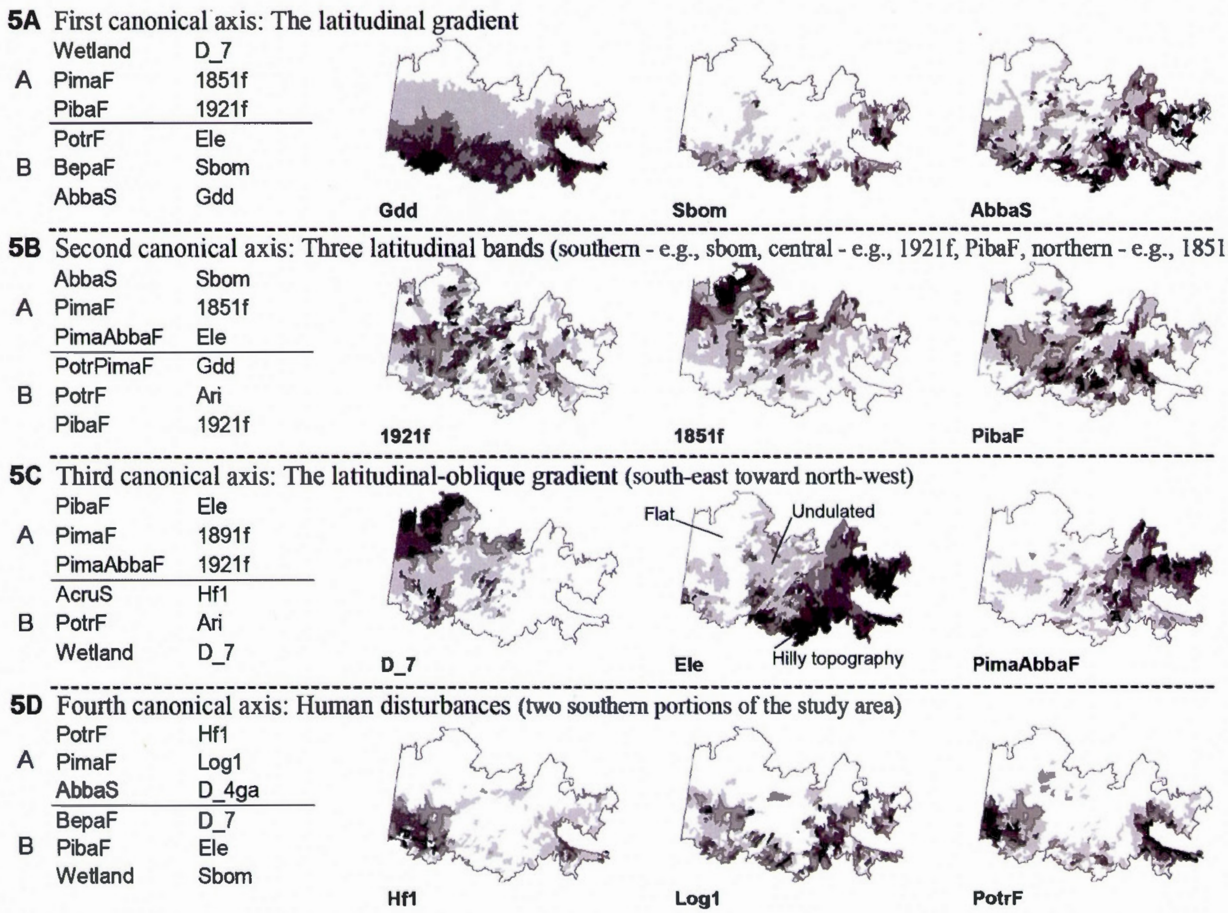


Figure 2.6 Gradual segmentation of the study area based on a *K*-means clustering (Fig. 2.2). Codes and description of forest types are presented in Table 2.2. The homogeneous landscape units defined in Fig. 2.7A are outlined in black

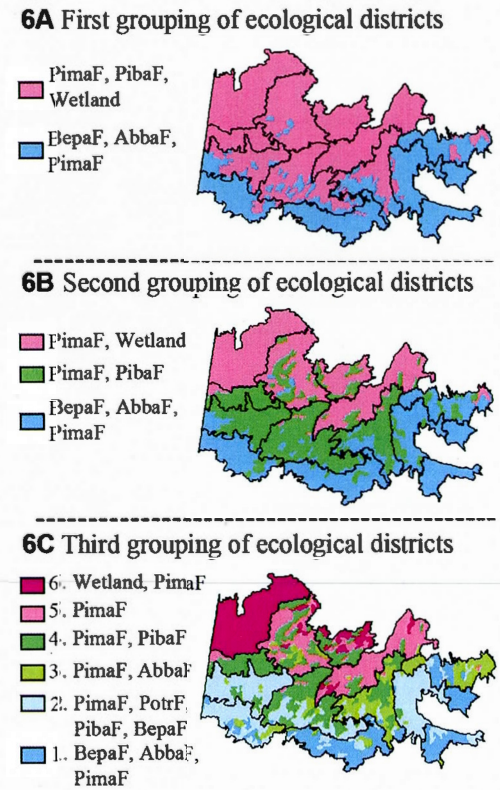
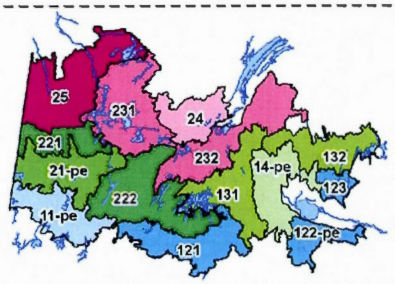


Figure 2.7 Ecological land classification of homogeneous landscapes units (ELCH). A) Map of homogeneous landscape units. B) Description of homogeneous landscape units at three levels of observation. C) Homogeneous landscape units positioned on an ordination diagram (ecological gradients) and described on disturbance histograms. The ordination diagram is related to the RDA (redundancy analysis) of two matrices: Y-vegetation and X-explanatory variables (Fig. 2.2)

7A



7B

Level I	Level II	Level III
Picea mariana-feathermoss domain	Northern portion	**25.** Peatlands and old *Picea mariana* forests
		24. *Picea mariana, Pinus banksiana* and peatlands. Young (mineral deposits) and old (organic deposits) forests
		23. *Picea mariana*, Old forests well represented (231-232)
	Southern portion	**22.** *Picea mariana, Pinus banksiana*. Young forests relatively abundant (221, 222)
		21-pe. *Picea mariana, Populus tremuloides, Pinus banksiana*. Strong anthropogenic influence
Abies balsamea-Betula papyrifera domain	Northern portion	**14-pe.** *Picea mariana, Populus tremuloides, Pinus banksiana, Betula papyrifera*. Strong anthropogenic influence
		13. *Picea mariana, Betula papyrifera, Abies balsamea*. Young (131, *Pinus banksiana*) and old (132) forests well represented
	Southern portion	**12.** *Betula papyrifera, Picea mariana*. Forests affected by insects outbreaks and fires (121, 122-pe, 123)
		11-pe. *Betula papyrifera, Picea mariana, Populus tremuloides*. Strong anthropogenic influence

7C

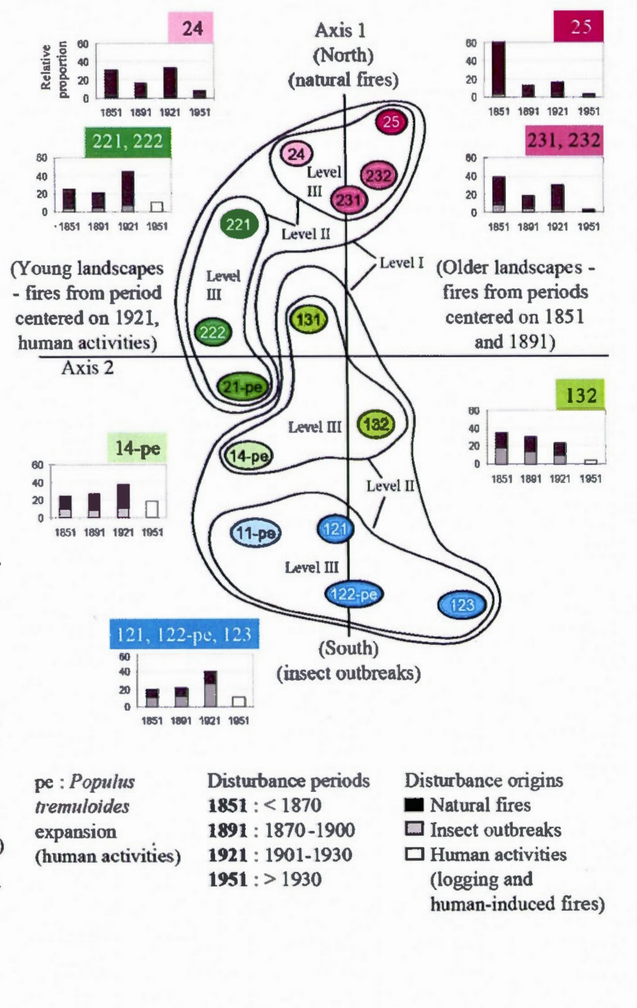
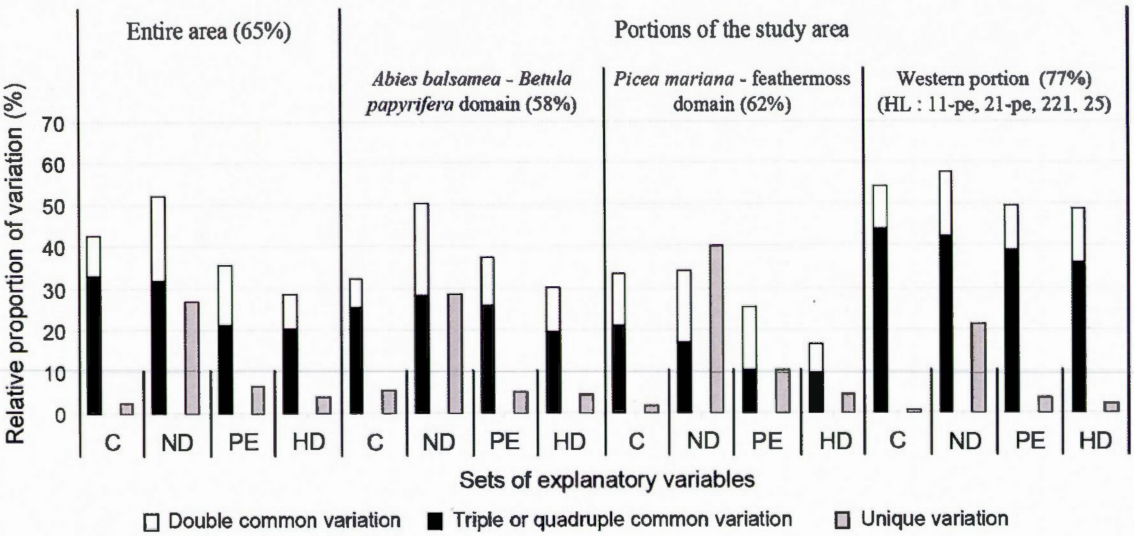


Figure 2.8 Relative proportion of vegetation variation (%) explained by each of the four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to the entire area and three of its portions. The variation explained by the four sets in each portion is indicated in brackets. The double common variation by a set is the sum of the double fractions containing this set (e.g., double common fraction of the set C = PE∩C + C∩ND + C∩HD). The triple common variation by a set is the sum of the triple fractions containing this set (e.g., triple common fraction of the set C = PE∩C∩ND + PE∩HD∩C + HD∩ND∩C) (Fig. 2.2)



	Entire area	*Abies balsamea - Betula papyrifera* domain	*Picea mariana* - feathermoss domain	Western portion
Unique variation by set				
Cu	2.6	5.5	1.7	0.7
NDu	26.9	28.6	40.0	21.3
PEu	6.7	5.1	10.2	3.7
HDu	4.1	4.5	4.4	2.3
Common variation by set				
Cc	42.9	32.3	33.5	54.7
NDc	52.4	50.6	34.1	58.0
PEc	35.7	37.5	25.5	49.9
HDc	28.9	30.3	16.5	49.0
Total variation by set				
Ct	45.5	37.8	35.2	55.4
NDt	79.4	79.2	74.1	79.3
PEt	42.5	42.6	35.6	53.6
HDt	33.0	34.8	21.0	51.4

Figure 2.9 Conceptual model comparing: 1) the traditional ELC (ecological land classification) approach based on climate (C) and physical environment (PE). Natural and human disturbances are considered a posteriori, 2) the proposed ELCH (ELC of homogeneous landscapes units). In this last approach, all the sets of variables are considered a priori, with special emphasis on natural (ND) and human disturbances (HD)

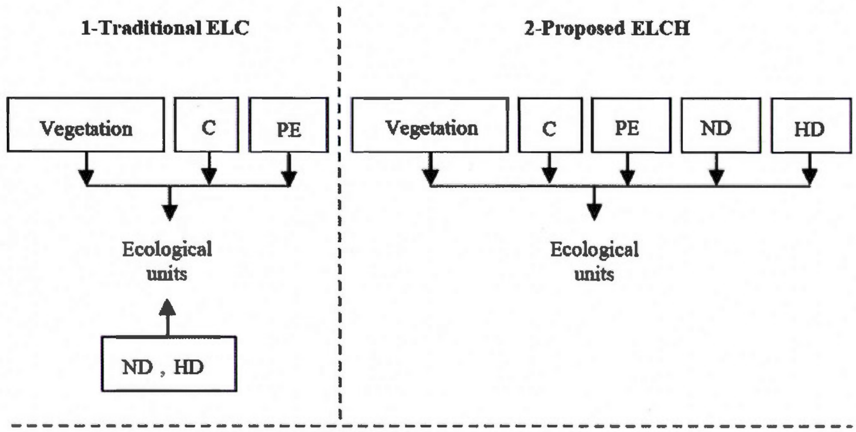


Table 2.1 Synthetic description of homogeneous landscape units. Codes and description of variables are presented on table 2.2.

		Natural homogeneous landscape units										Homogeneous landscape units affected by human activities			
		121	123	131	132	221	222	231	232	24	25	11-pe	122-pe	14-pe	21-pe
	Area (%)	7	2	8	6	4	11	11	10	5	12	6	3	7	7
Vegetation	BepaF	43	43	13	20	4	13	4	7	3	0	20	32	16	9
	AbbaF	4	9	4	11	0	1	0	2	0	0	1	3	3	1
	PimaAbba	3	9	7	12	1	2	1	5	1	0	1	4	5	2
	PotrF	7	9	5	4	16	7	6	1	2	1	23	31	23	21
	PibaF	10	3	22	8	19	26	8	11	24	4	6	3	20	16
	PimaF	25	21	38	38	41	33	59	57	40	33	25	18	25	34
Climate	Gdd	1295	1276	1210	1195	1201	1274	1165	1149	1139	1111	1345	1340	1281	1258
	Preci	342	359	328	346	312	334	312	330	316	287	303	345	316	312
Physical environment	Ele	77	90	56	73	23	39	25	38	26	11	27	70	64	24
	D_4ga	0	0	0	0	58	4	40	0	3	7	34	0	0	44
	D_7	1	1	4	2	16	12	13	9	23	59	17	2	1	18
Natural disturbances	Sbom	26	34	3	12	2	4	3	1	0	0	11	14	3	3
	1921f	15	7	24	14	45	33	31	23	32	16	19	14	29	37
	1891f	11	6	23	17	14	23	13	16	15	12	12	7	15	15
	1851f	11	10	16	17	28	18	29	32	30	60	10	5	13	19
Human disturbances	Log1	16	22	14	10	8	7	1	1	1	0	10	13	15	13
	Hfl	2	5	2	3	3	4	1	1	2	0	32	18	7	15
	Ag1-Fa1	0	0	0	0	0	0	0	0	0	0	5	3	0	6
	1951	11	9	10	4	5	13	0	0	0	0	16	7	28	14

Table 2.2 Codes and description of variables used to describe the homogeneous landscape units

	Code	Description
Vegetation	AbbaF	Relative area covered by *Abies balsamea* forest type
	AbbaS	Relative basal area for *Abies balsamea*
	AcruS	Relative basal area for *Acer rubrum*
	BepaF	Relative area covered by *Betula papyrifera* forest type
	PibaF	Relative area covered by *Pinus banksiana* forest type
	PimaF	Relative area covered by *Picea mariana* forest type
	PimaAbbaF	Relative area covered by *Picea mariana* and *Abies balsamea* forest type
	PotrF	Relative area covered by *Populus tremuloides* forest type
	PotrPimaF	Relative area covered by *Populus tremuloides* and *Picea mariana* forest type
	Wetland	Relative area covered by non-forested wetlands
Climate	Gdd	Annual number of growing degree-days
	Preci	Rainfall during the growing season (mm)
	Ari	Aridity index
Physical environment	Ele	Absolute difference of topographic elevation (m)
	D_4ga	Relative area covered by glaciolacustrine fine-textured (clay) surficial deposits
	D_7	Relative area covered by organic deposits
Natural disturbances	Sbom	Relative area covered by light spruce budworm outbreak (last outbreak 1975-1985)
	1921f	Relative proportion of forest inventory plots originating from fires between 1901 and 1930
	1891f	Relative proportion of forest inventory plots originating from fires between 1870 and 1900
	1851f	Relative proportion of forest inventory plots originating from fires before 1870
Human disturbances	Logl	Area covered by logging during the 1970s
	Hfl	Frequency of human-induced fires per $100km^2$ from 1938 to 1998
	Agl	Relative area covered by agriculture during the 1970s
	Fal	Relative area covered by fallow farmland during the 1970s
	1951	Relative proportion of forest inventory plots originating from logging since 1930

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2.9 Appendices

Appendix 1. Definition of the vegetation variables by theme (Y-matrix) (dans le contexte du doctorat, on renvoie le lecteur à l'appendice 1 du chapitre 1)

Appendix 2. Definition of the explanatory variables by set (X-matrix) (dans le contexte du doctorat, on renvoie le lecteur à l'appendice 2 du chapitre 1)

Appendix 3. Additional information on the ecological land classification of the study area

Appendix 4. Additional information on the description of homogeneous landscape units

Appendix 5. Additional information on the ecological land classification of homogeneous landscape units

Appendix 6. Recent history of human activities

Appendix 7. Recent history of human activities in the western portion of the study area (Abitibi)

Appendix 8. Additional information on the vegetation variation explained by four sets of explanatory variables (climate, natural disturbances, physical environment, and human disturbances) in the entire area and three of its portions

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APPENDIX 3

ADDITIONAL INFORMATION ON THE ECOLOGICAL LAND CLASSIFICATION OF THE STUDY AREA

In the main body of the paper, only the vegetation classification is presented. This appendix provides additional information on three other classifications: 3A, Physical environment, climate, and natural disturbances (E), 3B, Vegetation, physical environment, and climate (VPEC), and 3C, Vegetation, natural disturbances, and climate (VNDC). On maps, the homogeneous landscape units depicted in Figure 2.7A are outlined in black. Codes and description of variables are presented in Table 2.2 and in Appendices 1 and 2. Four main conclusions emerge:

1- The ecological land classification integrating all natural sets of explanatory variables (Appendix 3A) and the one based on vegetation, physical environment, and climate (Appendix 3B) are closely related to the vegetation classification (Fig. 2.3). The ecological entities vary mainly from the southeastern part of the study area to the northwestern part. The latitudinal-oblique gradient is well-expressed (Fig. 2.5C);

2- The ecological land classification based on vegetation, natural disturbances, and climate (Appendix 3C) is closely related to the three latitudinal bands described in the main body of the paper (Figs. 2.5B, 2.6B). Insect outbreaks (Sbom) and fires for the period centered on 1921 characterize the southern part, fires for the period centered on 1921 are abundant in the central part, and fires for the period centered on 1851 are dominant in the northern part. The independence of natural disturbances in these bands from changing conditions in other natural sets of variables is largely responsible for the high unique variation of vegetation explained by natural disturbances (Appendix 8). The ecological units (VNDC-1 to

VNDC-9) vary mainly from the south to north. The latitudinal gradient is well-expressed (Figs. 2.5A, 2.6A);

3- The ecological land classification presented in Appendix 3B is closely related to the second approach described in the introduction. This approach favours a classification based on vegetation, climate, and the physical environment. The ecological land classification presented in Appendix 3C is closely related to the third approach presented in the introduction, which emphasizes natural disturbances; and

4- In the description of the ecological land classification based only on vegetation, we stated that vegetation was a phytometer of environmental conditions (Fig. 2.3). The opposite is also true. An ecological land classification developed only using environmental variables is closely related to the vegetation (Appendix 3A). In different ways, both of these ecological classifications define the heterogeneity of the study area.

3A Ecological land classification based on the physical environment, climate, and natural disturbances

This classification, derived from a *K*-means clustering performed on explanatory variables of natural sets, is made up of 8 portions of territory. The southern and southeastern portions (E-1 to E-3) are characterized by a hilly topography (Ele > 40m) (Appendix 5d). Thin till and slopes exceeding 15 % are well-represented. Stands affected by the most recent spruce budworm outbreaks (Sbom) are abundant in the south (E-1). The central portion (E-4, E-5) is associated with an undulated topography (Ele 30-40m), fairly abundant lakes, and thick till. Coarse surficial deposits are scattered and old stands of the period centered on 1851 (1851f) are relatively abundant in E-4. These deposits reach their maximum in E-5, at nearly 20% of the area, and young stands dating from fires of the period centered on 1921 (1921f) are dominant. The western portion is defined by flat topography and an increasing abundance of wetlands, from south (E-6) to north (E-7, E-8, E-9). The proportion of glaciolacustrine fine-textured surficial deposits (D_4ga) and forest stands originating from fires of the period centered on 1921 (1921f) is high in E-7. In E-8, glaciolacustrine deposits are still abundant, but stands dating from fires of the period centered on 1851 (1851f) are well-represented. These old stands reach their maximum in the peaty *Picea mariana* stands of the northwestern portion (E-9). The climatic gradients overlap those of physical environment and natural disturbances. Along the latitudinal gradient, the number of annual growing degree-days exceeds 1250 in the south, but is less than 1200 in the north. Along the longitudinal gradient, aridity decreases from west to east.

3B Ecological land classification based on vegetation, physical environment, and climate

This classification, describing the relationships between vegetation, physical environment, and climate (VPEC), was developed using redundancy analysis (RDA, Legendre and Legendre 2012). The RDA was performed on the three vegetation themes of the Y-matrix (tree species, forest types, potential vegetation-successional stages) and the portion of the X-matrix containing physical environment and climate explanatory variables. The matrix of canonical axes resulting from the RDA was submitted to a *K*-means cluster analysis in order to delineate portions of the study area with similar links between vegetation, physical environment, and climate.

All of the southern and southeastern parts of the study area (portions VPEC-1 to VPEC-4) are characterized by a hilly topography (amplitude > 40 m). Thin till and slopes exceeding 15 % are well-represented. The transition towards the center of the territory (portions VPEC-6 and VPEC-7) is characterized by an undulating relief, with fairly abundant lakes, thick till, and slopes less than 10 %. The coarse surficial deposits are well represented locally in VPEC-6, but reach their maximum in VPEC-7, at nearly 25% of the area. The territory just southwest of Lac Mistassini (central portion of VPEC-8a) is characterized by abundant peatlands. The western part is defined by relatively flat topography and increasingly abundant wetlands, from the south (VPEC-4) to the north (VPEC-9). Clay surficial deposits dominate the northwestern part of the territory (VPEC-5 and VPEC-8a). All these spatial changes in vegetation and physical environment are also linked to changes in climate.

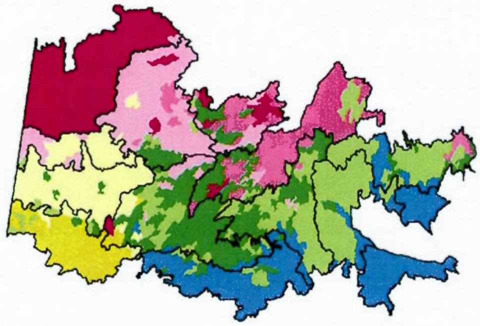
3C Ecological land classification based on vegetation, natural disturbances, and climate

This classification of vegetation, natural disturbances, and climate was assessed using a similar methodology as the previous classification, but with an X-matrix containing the explanatory variables of sets of natural disturbances and climate (VNDC). The following comments are limited to the natural disturbances. Stands affected by the last spruce budworm outbreaks and fires for the period centered on 1921 (1921f) are well-represented in the southern part of the territory (VNDC-1). The outbreaks also played a major role in VNDC-2b, in the northeastern. Elsewhere, fires take over as the dominant explanatory variable in forest dynamics. Signs of the impact of fires for the period centered on 1921 (1921f) form a long strip across the territory, from west to east (VNDC-3,5). Stands originating from the fires centered on 1851 (1851f) are present, but subdominant. The large band of territory formed by VNDC-3,5 is divided in the east by VNDC-2a, in which stands originating from fires from the period centered on 1851 (1851f) are slightly more abundant than those of the period centered on 1921 (1921f). Moreover, it is in the VNDC-7 portion that stands of the period centered on 1921 (1921f) are best-represented. The whole northern part of the study area is older and contains many stands originating from fires of the period centered on 1851 (1851f), in increasing abundance from VNDC-8 (44%) to VNDC-6 (63%) and to VNDC-9 (67%).

Appendix 3. Additional information on the ecological land classification of the study area. The homogeneous landscape units defined in Fig. 2.7A are outlined in black.

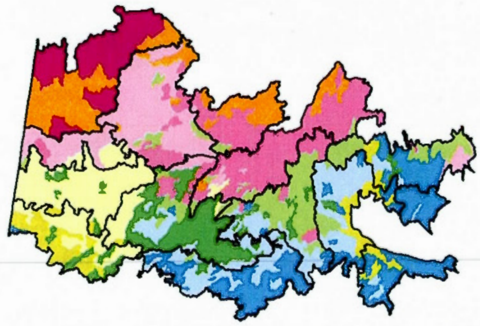
a. Ecological land classification based on the physical environment, climate and natural disturbances

	Sbom	1921f	1851f	Ele	D_4ga	Gdd
E-9:	0,	6,	67,	10,	6,	1102
E-8:	2,	30,	44,	18,	40,	1104
E-7:	2,	40,	15,	20,	50,	1290
E-6:	8,	30,	23,	42,	19,	1336
E-5:	1,	60,	16,	31,	3,	1279
E-4 :	1,	13,	63,	32,	3,	1157
E-2-3 :	3,	27,	33,	56,	4,	1182
E-1 :	22,	44,	21,	85,	0,	1290



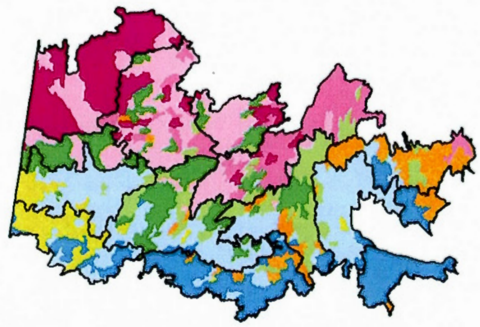
b. Ecological land classification based on vegetation, physical environment and climate

	Ele	D_4ga	Gdd
VPEC-9:	10,	6,	1102
VPEC-8b:	18,	10,	1104
VPEC-8a:	24,	46,	1174
VPEC-7:	31,	3,	1279
VPEC-6:	32,	3,	1157
VPEC-5:	20,	43,	1290
VPEC-4:	42,	19,	1336
VPEC-3:	62,	0,	1281
VPEC-2:	56,	4,	1182
VPEC-1:	85,	0,	1290



c. Ecological land classification based on vegetation, natural disturbances and climate

	Sbom	1921f	1851f
VNDC-9:	0,	6,	67
VNDC-8:	2,	30,	44
VNDC-7:	1,	60,	16
VNDC-6:	1,	13,	63
VNDC-4:	8,	30,	23
VNDC-3,5:	4,	36,	20
VNDC-2b:	14,	23,	38
VNDC-2a:	3,	27,	33
VNDC-1:	22,	44,	21



APPENDIX 4

ADDITIONAL INFORMATION ON THE DELIMITATION AND CODIFICATION OF HOMOGENEOUS LANDSCAPE UNITS

This appendix provides further information on the delineation of homogeneous landscape units presented in Figures 2.2 and 2.7 in the main part of the study. These units were first delineated by a visual analysis of the groups of ecological districts defined in Figure 2.6C, and according to the knowledge accumulated in this study, such as appendices 5, 6, and 7. The additional information presented in Figures 2.6A, 2.6B, and Figure 2.5 was used to describe and justify the landscapes delineated in Figure 2.6C, which considers six groups of ecological districts. We determined that this number was a good expression of the heterogeneity of the study area, based on an analysis of the overall distribution of the vegetation and explanatory variables. Further segmentation would achieve an excessively detailed level of analysis. The grouping of ecological districts (Fig. 2.6) is similar to the representation of the study area by canonical axes (Fig. 2.4). We used four axes to represent the territory, because a larger number of axes would provide excessive detail.

All landscapes coded with 1 as the first number form part of the *Abies balsamea-Betula papyrifera* domain.

- 11-pe (pale blue), in Figures 2.7A-2.7B-2.7C, is related to the southwestern area in Figure 2.6C. The northern delineation of 11-pe in Figures 2.7A is justified by Figure 2.6A, which shows a transition from dark blue to pale pink, corresponding to the limit between the *Abies balsamea-Betula papyrifera* and the *Picea mariana*-feathermoss domains. Appendix 3A (ecological land classification based on natural sets of explanatory variables) also suggests consideration of landscape 11-pe, as indicated in Figure 2.7A.

- 12 (dark blue) in Figures 2.7A-2.7B-2.7C corresponds to the dark blue area in Figure 2.6C. This landscape shows marked homogeneity with regard to its vegetation and explanatory variables (Fig. 2.7C). However, the dark blue characterizing the south is geographically separated (three patches). This disjunction is at the origin of the formation of landscapes 121, 122-pe, and 123. The main article explains why landscape 122 is qualified as *Populus* expansion (*pe*).

- 13 (dark lime green) in Figures 2.7A-2.7B-2.7C should be considered in relation to the area of the same color in Figure 2.6C. However, landscape 13 is segmented into two landscapes in Figures 2.6A and 2.6B. In Figure 2.6B, the western part of landscape 13 belongs to a large unit of dark green. This vast area is related to many variables, but mostly to the fires of the period centered on 1921. In Figure 2.6A, the western part of landscape 13 corresponds to the *Picea mariana*-feathermoss domain and the eastern part to the *Abies balsamea-Betula papyrifera* domain. On the basis of Figures 2.6A and 2.6B, it is justified to segment landscape 13 in Figures 2.6C and 2.7A into landscapes 131 and 132. These two landscapes show numerous affinities, as revealed by their close position on the ordination (Figure 2.7C). However, the position of landscape 131 in Figure 2.7C is high along axis 1, suggesting a close relationship with the *Picea mariana*-feathermoss domain. Because *K*-means clustering is not completely hierarchical, homogeneous landscape unit 131 is classified in the *Picea mariana*-feathermoss domain in Figures 2.6A and 2.6B, and in the *Abies balsamea-Betula papyrifera* domain in 2.6C. Considering the hilly topography (Ele > 40m, Appendix 5d), relative abundance of *Abies balsamea* (Appendix 6k), and grouping of homogeneous landscape unit 131 with homogeneous landscape 132 in some analyses (e.g. Fig. 2.3, Appendices 3A, 3B), we decided to classify homogeneous landscape 131 within the northern portion of the *Abies balsamea-Betula papyrifera* domain (Figure 2.7B). However, the landscape 131 is considered as relatively young because the high importance of stands originating from the fires of the period centered on 1921. The landscape 132, well supplied with stands originating from the fires of the period centered on 1891 and 1851 is classified as relatively old.

- 14-pe (pale lime green) in Figures 2.7A-2.7B-2.7C is related to the central-eastern pale blue area in Figure 2.6C. This landscape appears in dark blue in Figures 2.6A and 2.6B, confirming its close relation with the *Abies balsamea-Betula papyrifera* domain. Based on its pale blue color in Figure 2.6C and the information presented in Appendices 5 and 6, this landscape is classified as affected by human activities.

All landscapes coded with 2 as the first number (Figure 2.7) form part of the *Picea mariana*-feathermoss domain.

- 21-pe (pale green) in Figures 2.7A-2.7B-2.7C is related to the central-western pale blue area in Figure 2.6C. The southern delineation of 21-pe in Figures 2.7A and 2.6C is justified by Figure 2.6B showing a transition from dark blue to dark green and corresponding to the limit between the *Abies balsamea-Betula papyrifera* and *Picea mariana*-feathermoss domains. 21-pe is a landscape strongly affected by human activities, the others being 14-pe, 11-pe, and 122-pe. The proximity of these homogeneous landscape units, primarily 21-pe, 14-pe, and 11-pe, on the ordination in Figure 2.7C reveals their similarity.

- 22 (dark green) in Figures 2.7A-2.7B-2.7C corresponds with the dark green area in Figure 2.6B. However, the dark green area is geographically disjunct (two patches). This disjunction is at the origin of the formation of landscapes 221 and 222. The close position of these two landscapes in Figure 2.7C shows their similarity. Landscape 222 appears as a mosaic of pale blue and dark green in Figure 2.6C. The pale blue area of the southern part of 222 is closely related with the abundance of *Populus tremuloides* stands, whose origin is associated with human-induced fires that occurred along the railroad crossing the southern portion of the homogeneous landscape unit and connecting the Lac Saint-Jean and Abitibi regions (Figure 2.1).

The affinity of landscape 222 with human activities is also revealed by its proximity with others also strongly affected on the ordination diagram in Figure 2.7C.

- 23 (dark pink) in Figures 2.7A-2.7B-2.7C corresponds to the area of the same color in Figure 2.6C. However, the dark pink area is geographically disjunct (two patches). This disjunction is at the origin of the formation of landscapes 231 and 232. The close position of these two landscapes in Figure 2.7C shows their similarity. Landscape 232 is relatively homogeneous, as shown by its uniform dark pink color (Figures 2.6B, 2.6C), while 231 is more heterogeneous. The dark green color within landscapes 231 and 232 is related to *Pinus banksiana* stands and fires dating back to the period centered on 1921.

- 24 (pale pink) in Figures 2.7A-2.7B-2.7C is linked with a very patchy landscape in Figure 2.6C. Dark green is associated with *Pinus banksiana*, pale pink with *Picea mariana* on mesic soils, and purple with wetlands, forested or not. This landscape is much more homogeneous in Figures 2.6A and 2.6B. In these figures, emphasis is on the distinction between the two bioclimatic domains (Fig. 2.6A) and on two large bands strongly associated with natural disturbances in the *Picea mariana*-feathermoss domain (Fig. 2.6B).

- 25 (purple) in Figures 2.7A-2.7B-2.7C corresponds to the same color in Figure 2.6C. This landscape is homogenous. Hydric soils and old forests are abundant. Figures 2.6A and 2.6B justify considering this landscape as part of the *Picea mariana*-feathermoss domain.

Figure 2.6C shows six colors, corresponding to six groups of ecological districts. In Figures 2.7A-2.7B-2.7C, we identified nine colors. To explain this difference, we must consider that:

1- The pale blue area in Figure 2.6C is segmented into three homogeneous landscape units and colors: 11-pe, 21-pe (new color), and 14-pe (new color); and

2- The pale pink area (new color) in Figure 2.7B (landscape 24) corresponds to the grouping of 3 colored areas composing Figure 2.6C: pale pink, purple, and dark green.

The transition from 9 (Figure 2.7B) to 14 (Figures 2.7B, 2.7C) landscapes of level III is mainly justified by discontinuities in geographic distributions. For example, landscape 12 is divided into three landscapes occupying a specific portion of the southern part of the study area: 121, 122, and 123-pe. Some landscapes are also distinguished in reference to the entities delineated in Figures 2.6A and 2.6B. This is the case with landscape 13 which, although similar in Figure 2.6C (dark lime green), is separated into two landscapes in Figures 2.6A and 2.6B. It seems justified to maintain the two and three-number coding inside the level III of observation, because both express similar links between vegetation and explanatory variables. From the first to the third levels of observation, geographical entities become smaller in size. The landscapes remains at the level of the meso-scale; their delineation and description are based on the integration of several sets of explanatory variables (Appendix 8).

APPENDIX 5

ADDITIONAL INFORMATION ON THE DESCRIPTION OF HOMOGENEOUS LANDSCAPES UNITS

This appendix provides additional information on the integration of multiple sets of ecological gradients (Figures 2.4, 2.5) in the formation (Fig. 2.6) and description (Fig. 2.7) of the ecological land classification of homogeneous landscape units. On the maps of Appendix 5, the darker the gray, the greater the proportion of the variable. The homogeneous landscape units defined in Figure 2.7A are outlined in black.

Appendix 5a shows one of the main vegetation changes characterizing the homogeneous landscape units of the study area, which is the gradual decrease of *Abies balsamea-Betula papyrifera* potential vegetation (Ms2) from the south to the north of the study area. *Picea mariana* potential vegetation (Re2) shows an inverse distribution to Ms2.

Appendix 5b describes the gradual decline in the number of annual growing degree-days (Gdd). This decrease is the basis of 1) the latitudinal gradient characterizing the study area, and 2) the formation of the first canonical axis (Fig. 2.4A, Table 2.1). This variable, combined with others having a similar (e.g. Sbom, Ele, Table 2.1) or inverse distribution (e.g. D_7, 1851f), allows us to subdivide the study area into the *Abies balsamea-Betula papyrifera* domain (south) and the *Picea mariana*-feathermoss domain (north) (Figure 2.6A).

Appendix 5c contrasts stands evolving under the effects of 1) insect outbreaks (1921o), 2) fires from the period centered on 1921 (1921f) with post-fire vegetation dominated by early-successional species (*Pinus banksiana, Betula papyrifera, Populus tremuloides*), and 3) fires (1851f) and insect outbreak (1851o) from the period centered on 1851. These explanatory variables are largely responsible for the three longitudinal bands characterizing the study area: the south (landscapes 11-pe, 121, 122-pe, 123), center (landscapes 21-pe, 221, 222, 131, 132, 14-pe), and north (landscapes 231, 232, 24, 25). These bands are clearly identified in Figure 2.4B, which describes the second canonical axis of ecological districts and their grouping (Fig. 2.6C) in order to delineate homogeneous landscape units.

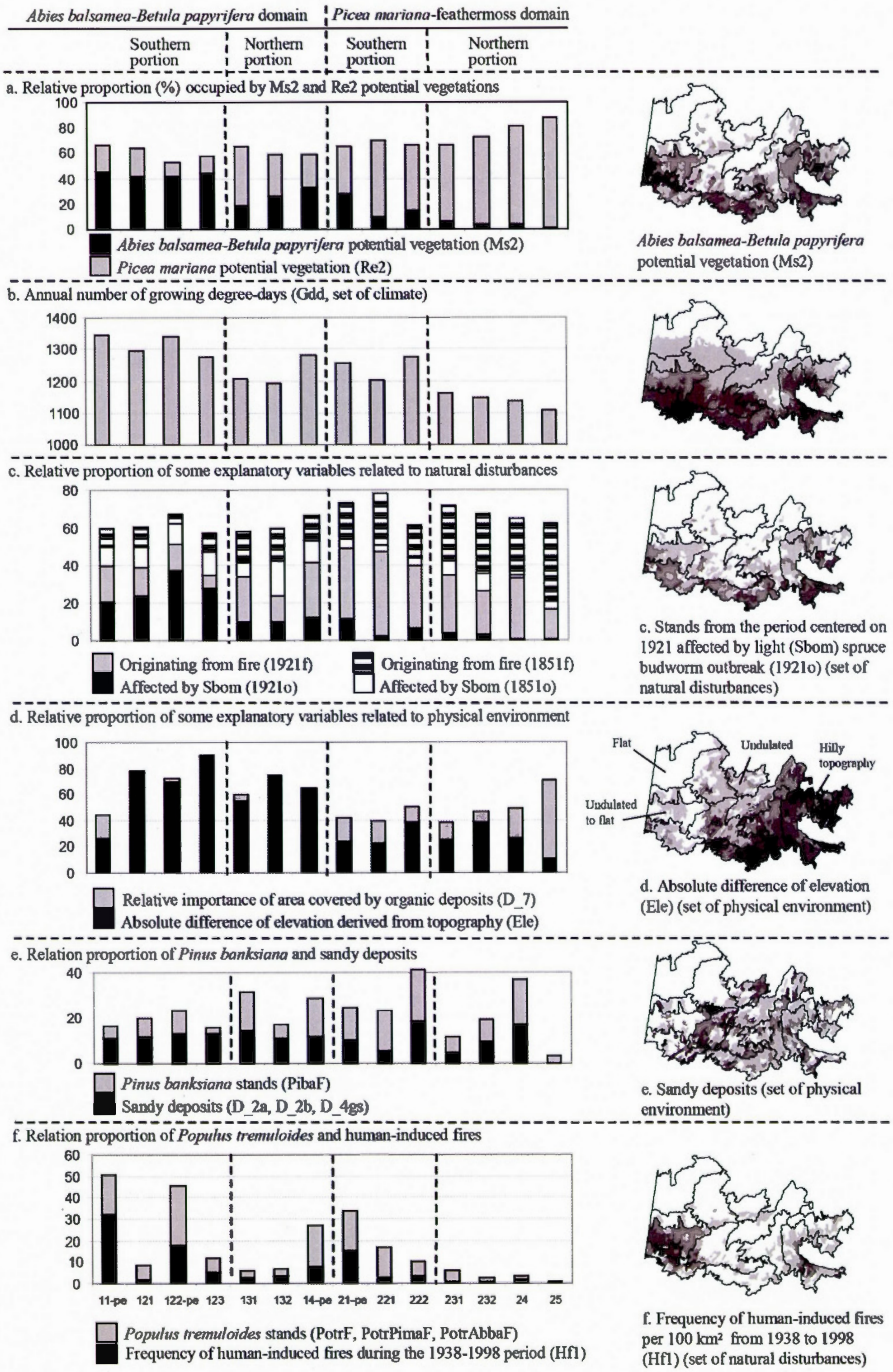
Appendix 5d shows the differences between the two bioclimatic domains with regard to topography. Throughout almost all the *Abies balsamea-Betula papyrifera* domain, the elevation (Ele, Table 2.1, Figures 2.4C, 2.5C) reaches a value around 60-80 m, indicating the presence of a well-expressed relief (hilly topography). This value drops to less than 40 m in the *Picea mariana* domain, indicating an undulated to flat topography. In the latter domain, peatlands (D_7) generally occupy between 10 and 20% of the area. Homogeneous landscape unit 25 is an exception, with wetlands covering nearly 60% of this homogeneous landscape. These changes in the physical environment are critical in the formation of the third canonical axis of the RDA (Fig. 2.4C) and the subdivision of the territory into six groups of ecological districts (Fig. 2.6C).

Appendix 5e shows the relation between the proportion of sandy deposits and the proportion of *Pinus banksiana*. Even if topography differs between homogeneous landscape units 131, 14-pe (hilly topography - *Abies balsamea-Betula papyrifera* domain) vs 21-pe, 221, 222, 24 (undulating to flat topography - *Picea mariana*-feathermoss domain) (Fig. 2.7A), the high proportion of sandy surficial deposits still supports the development of a relatively large population of *Pinus banksiana.* Ultimately, the homogeneous landscape units forming the broad central band (131, 14-pe, 21-pe, 221, 222) are similar in terms of 1) climate (1200 growing degree-days), 2) natural disturbances (abundance of stands originating from fires that occurred during the period centered on 1921: 1921f), 3) some elements of the physical environment (sandy surficial deposits), and 4) abundance of *Pinus banksiana*. Along this large band, natural disturbances remain similar (1921f), even if the topography changes from undulating to hilly in the east, to undulating-flat in the west. This similarity, mainly expressed by natural disturbances, explains the overwhelming role of this set in this study. However, as a general rule, there is a synchronicity of changes in vegetation along the ecological gradients, demonstrated by the high proportion of vegetation variation explained by the double, triple, and quadruple combinations of natural disturbances with other sets of explanatory variables (Appendix 8).

Appendix 5f shows how human disturbances overlap the natural sets of explanatory variables in some homogeneous landscape units. The consequences of human activities are primarily observed in the two southern extremities of the study area and are mostly defined by the frequency of human-induced fires per 100 km^2 from 1938 to 1998 (Hf1, Fig. 2.5D), as well as the area affected by logging (Log1, Fig. 2.5D). Human activities are the basis of the fourth canonical axis (Fig. 2.4D) and the delineation of four homogeneous landscapes (Fig. 2.6C, Fig. 2.7, landscapes 11-pe, 122-pe, and14-pe, 21-pe).

Finally, Appendices 5g to 5m present the 14 homogeneous landscape units with regard to their descriptive and explanatory variables.

Appendix 5. Additional information on the ecological land classification of homogeneous landscape units (ELCH).



Appendix 5 (continued). Description of homogeneous landscape units

g. Relative proportion of species in the homogeneous landscape units (forest inventory plots). Codes are presented in appendix 1.

	Hardwood				Coniferous species				
	AcruS BealS	BepaS	PotrS	SaspS	PiglS	PimaS	PibaS	AbbaS	ThocS
11-pe	1.1	18.6	22.6	3.2	3.0	29.5	6.0	14.0	1.1
121	1.7	24.3	5.7	0.2	3.2	32.2	7.4	24.6	0.2
122-pe	6.0	18.8	18.2	1.1	5.2	24.4	3.1	21.5	0.3
123	5.9	28.1	2.8	0.2	4.5	27.1	2.2	28.1	0.0
131	0.6	13.4	4.5	0.1	0.8	51.1	12.8	16.6	0.0
132	0.0	15.7	2.8	0.1	2.0	51.9	3.2	24.1	0.0
14-pe	0.8	20.1	16.9	0.6	1.7	30.9	17.7	10.6	0.2
21-pe	0.2	8.7	18.4	2.7	1.4	40.9	15.9	11.1	0.1
221	0.0	3.2	13.6	1.2	0.7	59.7	18.0	3.1	0.0
222	0.2	12.7	6.6	0.4	0.8	50.3	21.0	7.5	0.0
231	0.0	3.7	5.4	0.4	0.5	77.1	6.6	6.0	0.0
232	0.0	5.6	1.3	0.1	0.4	76.9	7.1	8.4	0.0
24	0.0	4.2	2.6	0.2	0.3	74.0	16.2	2.2	0.0
25	0.0	0.6	2.1	0.2	0.3	88.8	5.0	2.3	0.3

h. Relative proportion of forest types in the homogeneous landscape units (geobase SIFORT-2, 1980-1990). Codes are presented in appendix 1.

	Hardwood			Mixedwood				Coniferous stands				Others			Totals	
	BepaF	BealF	PotrF	Bepa PimaF	Bepa AbbaF	Potr PimaF	Potr AbbaF	PimaF	Pima AbbaF	PibaF	AbbaF	Alru	Wet-land	Heath -land	tot_ Bepa	tot_ Potr
11-pe	6.0	0.3	13.1	11.7	2.4	0.0	0.9	25.2	1.3	6.4	1.4	5.7	13.7	3.0	20.1	14.1
121	15.9	0.6	3.6	15.5	11.5	0.0	0.7	25.3	3.5	10.5	3.7	1.3	4.5	0.6	42.8	4.3
122-pe	14.1	2.9	14.2	9.9	7.9	0.0	7.3	18.1	3.6	3.3	2.6	2.6	2.9	1.1	31.8	21.5
123	10.0	3.0	3.7	14.7	18.4	0.0	0.5	21.0	8.5	3.1	9.1	0.5	2.4	0.7	43.1	4.2
131	2.8	0.0	1.5	7.6	2.4	0.0	0.3	37.9	7.0	22.0	4.5	1.4	8.2	1.6	12.8	1.8
132	3.0	0.0	1.5	8.9	8.1	0.0	0.2	38.0	11.6	7.6	11.4	1.3	3.7	2.6	20.1	1.6
14-pe	6.1	0.2	11.8	7.2	2.4	0.0	0.7	24.9	4.7	20.2	3.2	1.7	4.4	2.5	15.6	12.5
21-pe	2.6	0.0	7.3	5.3	1.0	0.0	0.4	34.2	2.5	16.0	0.7	4.6	11.2	1.2	9.0	7.7
221	1.0	0.0	2.7	2.3	0.4	0.0	0.3	40.7	1.0	19.1	0.2	2.8	16.4	0.7	3.7	3.0
222	2.9	0.0	2.2	8.1	2.4	0.0	0.5	32.8	2.4	26.1	1.0	1.7	14.6	0.7	13.4	2.7
231	0.7	0.0	1.8	3.4	0.4	0.0	0.1	58.8	1.3	8.1	0.2	3.7	16.0	1.5	4.5	1.8
232	1.1	0.0	0.3	5.2	0.9	0.0	0.1	56.7	5.1	10.9	1.8	1.3	13.8	1.8	7.2	0.3
24	0.6	0.0	0.6	2.3	0.2	0.0	0.0	40.2	0.7	24.1	0.1	2.0	25.2	3.0	3.1	0.6
25	0.0	0.0	0.1	0.1	0.0	0.0	0.0	32.7	0.4	3.6	0.1	0.7	59.8	2.0	0.1	0.1

Appendix 5 (continued 2). Description of homogeneous landscape units

i. Relative proportion of potential vegetation and successional stages in the homogeneous landscape units (forest inventory and ecological inventory plots). Codes are presented in appendix 1.

			MS2					RS2					RE2				
	MS1	RS1	S2	S3	S4	S5	tot	S2	S3	S4	S5	tot	S2	S3	S4	S5	tot
11-pe	4.2	2.2	29.8	6.9	4.5	4.1	45.2	8.2	5.8	5.2	7.9	27.0	16.1	0.9	1.4	3.0	21.4
121	5.8	0.3	12.3	12.5	8.4	8.5	41.6	7.4	5.5	7.0	10.3	30.2	16.0	1.8	2.4	1.8	22.1
122-pe	16.9	4.3	17.8	13.4	6.4	4.5	42.1	6.5	5.1	5.2	9.4	26.1	9.0	0.3	0.4	1.0	10.7
123	17.5	0.3	8.8	11.4	12.4	12.1	44.7	5.4	2.4	3.2	13.3	24.4	10.7	0.0	0.1	2.2	13.0
131	1.0	0.0	7.1	3.2	3.3	4.7	18.4	9.7	5.9	5.9	12.4	33.9	29.5	4.9	4.9	7.5	46.6
132	0.2	0.0	6.0	4.7	5.0	9.7	25.4	9.1	4.4	5.2	21.9	40.5	22.2	1.6	2.7	7.4	33.9
14-pe	2.6	1.6	24.0	4.5	2.2	2.5	33.1	12.6	10.6	7.3	5.9	36.5	18.3	2.6	4.1	1.3	26.3
21-pe	1.0	0.4	17.6	4.7	2.1	3.7	28.2	9.6	7.9	6.5	9.0	33.0	25.3	3.4	3.6	5.2	37.5
221	0.0	0.0	7.5	0.9	0.5	0.9	9.9	11.0	6.7	6.7	4.9	29.4	29.4	5.4	6.7	19.3	60.8
222	0.9	0.1	8.4	3.0	2.3	1.1	14.7	10.2	8.2	7.2	6.8	32.4	29.1	5.9	7.5	9.5	51.9
231	0.0	0.0	3.0	1.8	0.6	0.3	5.6	12.4	3.5	5.8	11.2	33.0	33.4	2.6	3.9	21.6	61.5
232	0.0	0.3	1.3	0.8	0.8	1.0	3.9	6.2	3.6	3.6	13.4	26.7	31.4	2.7	5.4	29.6	69.1
24	0.0	0.1	2.9	0.3	0.1	0.3	3.6	6.1	2.9	4.4	4.5	17.9	39.3	6.2	10.0	23.0	78.5
25	0.0	0.6	0.7	0.0	0.0	0.2	0.9	4.8	1.0	1.4	5.2	12.3	44.5	1.7	2.5	37.6	86.3

j. Physical environment. Codes are presented in appendix 2.

	Physiography						Surficial deposits									Other
	Malt	S_a	S_b	S_c	S_d	Ele	D_1a	D_1ar	D_2a	D_2b	D_4ga	D_4gs	D_7	D_wa	D_[illegible]	L_100km²
11-pe	319	81	13	4	2	27	4	13	2	0	34	9	17	8	11	0.8
121	467	38	16	25	18	77	39	34	2	9	0	0	1	7	6	0.8
122-pe	373	51	15	17	14	70	42	32	2	9	0	2	2	7	2	0.8
123	368	29	21	24	20	90	24	46	4	9	0	0	1	9	6	0.5
131	469	53	21	14	9	56	43	21	4	10	0	0	4	12	5	1.3
132	394	34	25	22	16	73	42	29	3	8	0	0	2	9	5	0.8
14-pe	404	38	27	19	12	64	42	31	4	7	0	0	1	4	10	0.4
21-pe	321	85	10	4	1	24	8	10	2	0	44	9	18	3	6	0.3
221	301	82	12	4	2	23	6	5	1	0	58	5	16	2	7	0.1
222	401	71	14	10	4	39	39	14	5	7	4	7	12	10	2	1.2
231	293	71	17	9	3	25	19	9	1	0	40	4	13	10	4	0.5
232	425	75	14	7	3	38	54	10	5	4	0	2	9	11	3	1.5
24	360	77	14	6	3	26	35	7	6	6	3	5	23	8	2	1.2
25	243	92	5	2	1	11	3	1	0	0	7	0	59	9	3	0.7

Appendix 5 (continued 3). Description of homogeneous landscape units

k. Natural disturbances. Codes are presented in appendix 2.

	Spruce budworm outbreaks						Fires						Other
	Sbon	Sbom	Sbos	1921o	1891o	1851o	Fia	Fif	1951	1921f	1891f	1851f	Wi
11-pi	14	10.6	1.8	21	7	10	3.3	1.0	0	19	12	10	0.1
121	19	26.1	2.9	24	13	11	3.7	1.4	0	15	11	11	0.5
122-pi	26	13.8	2.3	38	8	11	0.9	0.9	0	14	7	5	0.1
123	21	33.6	2.5	28	18	12	1.7	0.8	0	7	6	10	0.0
131	8	2.7	0.4	10	10	8	6.3	1.2	0	24	23	16	0.3
132	11	12.4	0.5	10	14	19	4.8	2.1	0	14	17	17	0.7
14-pi	6	2.8	0.2	13	7	12	7.0	1.1	0	29	15	13	0.1
21-pi	3	3.0	0.8	12	6	5	2.0	0.3	0	37	15	19	0.3
221	2	1.8	0.1	3	1	3	1.9	0.5	0	45	14	28	1.1
222	7	3.5	0.6	7	6	4	2.1	0.8	0	33	23	18	0.8
231	5	2.8	1.4	4	5	8	4.4	1.1	3	31	13	29	2.1
232	4	0.7	0.1	3	5	9	3.0	1.7	4	23	16	32	1.3
24	1	0.0	0.0	1	2	2	6.9	1.6	9	32	15	30	0.3
25	0	0.0	0.0	0	1	4	6.2	0.9	3	16	12	60	0.2

l. Human disturbances. Codes are presented in appendix 2.

	Logging			Fire			Agriculture	
	1951	Log1	Log2	Hf2	Hf1	Fa1	Ag1	Ag2
11-pe	16.0	10.3	9.3	60.3	32.1	2.1	3.0	2.4
121	11.0	16.0	13.6	19.2	2.0	0.0	0.0	0.0
122-pe	7.0	13.1	12.7	8.3	18.0	0.6	2.1	1.6
123	9.0	22.2	28.3	52.0	4.8	0.0	0.0	0.0
131	10.0	14.0	20.1	45.8	2.4	0.0	0.0	0.0
132	4.0	9.8	22.8	25.2	3.1	0.0	0.0	0.0
14-pe	28.0	15.0	18.9	63.2	7.3	0.1	0.1	0.1
21-pe	14.0	13.1	21.7	16.3	15.4	2.5	3.7	2.8
221	5.0	8.2	19.5	2.7	2.8	0.0	0.0	0.0
222	13.0	7.1	9.4	35.5	3.8	0.2	0.2	0.3
231	0	0.9	12.1	2.0	1.0	0.0	0.0	0.0
232	0	0.8	4.6	3.1	0.9	0.0	0.0	0.0
24	0	0.6	5.0	5.7	1.6	0.0	0.0	0.0
25	0	0.0	0.1	7.1	0.1	0.0	0.0	0.0

m. Climate. Codes are presented in appendix 2.

	Longitudinal gradient			Latitudinal gradient				
	Preci	Vpd	Ar	Gdd	Mat	Dwf	Dwfc	Ef
11-pe	303	1381	2.1	1345	1.0	175	95	248
121	342	1270	1.5	1295	0.7	174	95	247
122-pe	345	1288	1.5	1340	1.4	178	101	250
123	359	1263	1.2	1276	0.6	174	97	249
131	328	1224	1.4	1210	0.1	169	92	245
132	346	1210	1.1	1195	-0.1	168	94	247
14-pi	316	1274	1.5	1281	0.6	173	96	248
21-pi	312	1312	1.6	1258	0.5	175	91	243
221	312	1298	1.4	1201	0.0	167	85	242
222	334	1297	1.5	1274	0.4	173	94	247
231	312	1263	1.5	1165	-0.6	165	85	242
232	330	1198	1.3	1149	-0.6	164	90	242
24	316	1202	1.4	1139	-0.7	165	86	242
25	287	1254	1.9	1111	-0.9	165	85	239

APPENDIX 6

RECENT HISTORY OF HUMAN ACTIVITIES

This appendix provides additional information on human activities. Our goals are to: 1) distinguish the effects of natural disturbances from those of human disturbances and, 2) characterize homogeneous landscape units with respect to the loss of integrity caused by human activities during the last part of 19^{th} century and throughout the 20^{th} century. Two new variables were created. The first is a combination of the forest type and the central year of the period of origin (e.g. PotrF_1951: the *Populus tremuloides* forest type, originating from human activities undertaken after 1930). The second is a combination of the forest type and the relative proportion (basal area) of species (e.g. PotrF_abba: relative proportion of basal area of *Abies balsamea* in *Populus tremuloides* forest stands). Three species were considered: *Abies balsamea* (Abba), *Populus tremuloides* (Potr), and *Picea mariana* (Pima). Subsequently, the two new descriptive variables were gathered in a matrix of vegetation (Y-matrix) and used with an X-matrix of explanatory variables to achieve a redundancy analysis (RDA). The latter X-matrix is the same as that used to describe the four sets of explanatory variables (Fig. 2.2). The result of this analysis is presented in an ordination diagram on which the vegetation variables are positioned. The arrows indicate the direction of vegetation change. The thematic maps of human activities, the histograms, and the ordination diagram were used to reconstruct the history of *Populus tremuloides* expansion (pe), *Abies balsamea* expansion (ae), and increase of young *Picea mariana* and *Pinus banksiana* stands in the study area. The darker the gray color on the maps, the greater the proportion of the variable. The homogeneous landscape units outlined on maps (black lines) are presented in Figure 2.7 and in Appendix 6.

Populus tremuloides expansion (pe) (Appendices 6a to 6f, 6p, 6q and 6y)

Populus tremuloides expansion occurred mainly on clay (southwestern portion), but also on glacial surficial deposits (till, southeastern portion) in the study area. Appendices 6a-6p (human-induced fires, Hf1), 6b-6p (logging, Log1), and 6y (stands of the period centered on 1951) give a first overview of the distribution and intensity of human disturbances. This impact seems to be recent, as suggested by the limited geographical distribution of *Populus tremuloides* in the early 20th century (Appendices 6c, 6q, PotrF_1921), when human activities were initiated and then intensified. It is estimated that the increase in *Populus tremuloides* would have occurred between the end of the 19th century and approximately 1940, in response to human-induced fires and logging. *Populus tremuloides* stands affected by these human activities have been grouped within the variable PotrF_1951. Comparison of the thematic map (Appendix 6d) and histogram (Appendix 6q) of the latter variable with the thematic map (Appendix 6c) and histogram (Appendix 6q) of *Populus tremuloides* from the period centered on 1921 (PotrF_1921) suggests an important expansion in the geographical distribution and abundance of *Populus* in the southern portion of the territory. Appendix 6q shows that close to 20% of the *Populus tremuloides* stands originated from fires of the period centered on 1921 in homogeneous landscape units affected by human activities, compared to 30 to 60% from human activities (period centered on 1951). The successional vector between the variable PotrF_1921 and PotrF_1951 (Appendices 6v to 6y) indicates that the relatively large distribution and low abundance of *Populus tremuloides* stands during the period centered on 1921 became concentrated and highly abundant in the southern part during the period centered on 1951.

Under the effects of logging, the increase in *Populus tremuloides* could potentially continue northward as far as the forest type characterized by this hardwood species is present in the landscape (Appendix 6e, PimaF_potr). This dynamic could possibly characterize the whole clay plain of Abitibi. Glacial deposits (in the eastern section) should be less affected by *Populus* expansion. Finally, landscapes dominated by peatlands should escape this process and be clearly dominated by *Picea mariana*. The scarcity of *Populus tremuloides* in the northwest portion of the territory supports this assumption (Appendix 6f).

Abies balsamea expansion (Appendices 6g to 6k, 6r and 6s)

Human activities also promote *Abies balsamea* expansion. *Populus tremuloides* and *Abies balsamea* expansions are two closely-related processes characterizing the same territories (Grondin and Cimon 2003, Laquerre et al. 2009, Arbour and Bergeron 2011). Forest inventory plots reveal that in the early 20th century, when human activities were getting underway in the southern portion of the study area, *Abies balsamea* was distributed mainly in the southern portion affected by the insect outbreak of the early 20th century (from 1910 to 1920) (Appendix 6g). The *Abies balsamea* expansion would have occurred later, as a result of logging. In the context of this study, *Abies balsamea* stands linked to mid 20th century human activities (logging: 1930 and later) and to the spruce budworm outbreak of the second half of the 20th century could not be distinguished and were integrated into the AbbaF_1951 variable (Appendix 6h). We estimate that the majority of AbbaF_1951 stands originated from logging because of the low severity of the 1950-1960 spruce budworm outbreak. The majority of these stands contain older trees, which allows us to link their origin with earlier outbreaks (AbbaF_1921, AbbaF_1891). The *Abies balsamea* increase hypothesis is based on these elements:

1- There is a strong relationship between the distribution of *Abies balsamea* in the period centered on 1951 (Appendix 6h) and logging (Appendix 6b). This link suggests that some stands of *Abies balsamea* dating from this priod would have developed following logging in various types of forest cover well-populated with

Abies balsamea. The successional vector linking some forest cover dominated or sub-dominated by *Abies balsamea* (e.g. PotrF_abba) to *Abies balsamea* stands from the period centered on 1951 (AbbaF_1951) (Appendices 6v to 6y) shows the abundance of *Abies* in the southern portion of the territory;

2- There is both an abundance of *Abies balsamea* in *Populus tremuloides* stands (PotrF_abba) (Appendices 6i, 6r) and a similarity in terms of geographical distribution between *Populus tremuloides* from the period centered on 1951 (Appendix 6d) and *Abies balsamea* from the same period (Appendix 6h). It is assumed that *Populus tremuloides* stands originating from fires are mainly pure stands of *Populus tremuloides* (Potr) or *Populus tremuloides* with *Picea mariana* (Potr_PimaF), while *Populus tremuloides* and *Abies balsamea* stands (Potr_AbbaF) are more related to logging; and

3- There is a relatively high abundance of *Abies balsamea* stands dating from the period centered on 1951 in homogeneous landscape units affected by human activities (25-35%, Table 2.1, Appendix 6s), compared to less than 25% in natural landscapes. It is estimated that the increase in geographical distribution and abundance of *Abies balsamea* and *Populus tremuloides* led to an increase in the proportion of stands of *Abies balsamea-Betula papyrifera* potential vegetation (Ms2). This increase was mainly observed in the 21-pe homogeneous landscape unit (Appendix 5a). This dynamic, identified in the ecological land inventory of the Ministère des ressources naturelles du Québec (MRN) (1985-1995), is probably an important input in the delineation of the northern limit reached by the *Abies balsamea-Betula papyrifera* bioclimatic domain. This limit is located at the junction between 21-pe and 221 homogeneous landscape units, and corresponds to the expansion zone of:

1- human-induced fires (Appendix 6a);

2- logging during the 1970s (Appendix 6b);

3- *Populus tremuloides* stands from the period centered on 1951 (Appendix 6d);

4- *Abies balsamea* stands from the period centered on 1951(Appendix 6h);

5- *Abies balsamea* in *Populus tremuloides* stands (PotrF_abba, Appendix 6i); and

6- stands classified with Ms2 potential vegetation (Appendix 5a).

It is hypothesized that the contemporary natural northern limit of the *Abies balsamea-Betula payrifera* domain would correspond to the northern limit of homogeneous landscape unit 11-pe (Fig. 2.7A). In addition, we anticipate an expansion of *Abies balsamea* in the northern part of Abitibi, as far as *Populus tremuloides* is well-represented in *Picea mariana* stands (Appendix 6e) and *Populus tremuloides* stands are present. However, the most northern *Populus tremuloides* stands contain only a very small percentage of *Abies balsamea* (Appendix 6i).

Several factors also suggest an expansion of *Abies balsamea* in the eastern section of the study area, where it is naturally well represented because of relatively high rainfall and a hilly topography. The hypothesis that *Abies balsamea* will increase is based on the close relationship between:

1- the abundance of logging (Appendix 6b) and a high proportion of *Abies balsamea* stands (AbbaF) (Appendix 6k). Logging has been underway for several decades (1930-1970) in the Gouin Reservoir region (a vast reservoir located in the southcentral part of the study area, Fig. 2.7A) and in the northern part of the Lac Saint-Jean region; and

2- the abundance of *Abies balsamea* in *Picea mariana* stands (Pima_abba), especially in homogeneous landscape units 231 and 232 (Appendix 6r).

Young *Picea mariana* stands and young *Pinus banksiana* stand expansion (Appendices 6l to 6o, 6t, and 6u)

Human activities influenced forest dynamics, resulting in a passage from old coniferous to young coniferous stands. These stands are classified within the period centered on 1951 (set of human disturbances). We hypothesized that the abundance of forest stands of the period centered on 1951, dominated by *Picea mariana* or *Pinus banksiana,* originated from human activities. This hypothesis is based on:

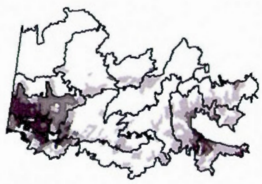
1- the correspondence between the geographical distribution of *Picea mariana* stands (Appendix 6m, PimaF_1951) and *Pinus banksiana* stands (Appendix 6o, PibaF_1951) for the period centered on 1951 with human-induced fires (Appendix 6a) and logging (Appendix 6b);

2- the transformation from a widespread distribution during the period centered on 1921 to a southern distribution during the period centered on 1951 for *Picea mariana* (Appendices 6l and 6m) and *Pinus banksiana* (Appendices 6n, 6o). The tendency of stands of the period centered on 1951 to prevail in the southern portion of the study area is also suggested by the ordination of the successional vectors between *Pinus banksiana* and *Picea mariana* stands in the period centered on 1921 (PimaF_1921, PibaF_1921) toward the period centered on 1951 (PimaF_1951, PibaF_1951) (Appendices 6v to 6y); and

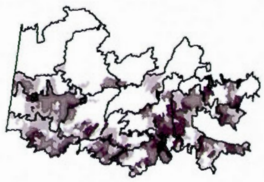
3- the difference in abundance of young stands of *Pinus banksiana* (Piba_1951) and *Picea mariana* (Pima_1951), from high in homogeneous landscape units affected by human activities, to low in natural landscapes of the same stands (Appendices 6t, 6u).

Appendix 6. Recent history of human activities

Human activities

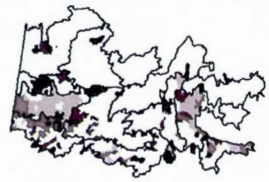


a. Frequency of human-caused fires per 100km² from 1938 to 1998 (Hfl)

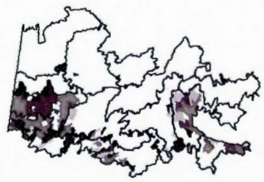


b. Logging during the 1970s (Log1)

***Populus tremuloides* expansion**

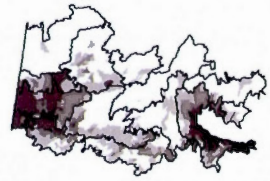


c. *Populus tremuloides* stands for the period centered on 1921 (PotrF_1921)



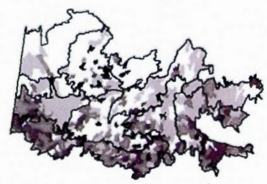
d. *Populus tremuloides* stands from the period centered on 1951 (PotrF_1951)

e. Relative proportion (basal area) of *Populus tremuloides* in *Picea mariana* stands (PimaF_potr) (basal area maximum value: 10%)

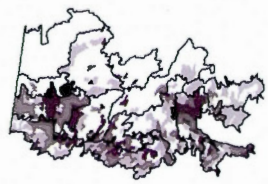


f. *Populus tremuloides* stands (PotrF, PotrPimaF, PotrAbbaF)

***Abies balsamea* expansion**



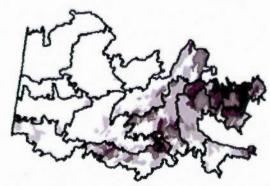
g. *Abies balsamea* stands from the period centered on 1921 (AbbaF_1921)



h. *Abies balsamea* stands from the period centered on 1951 (AbbaF_1951)

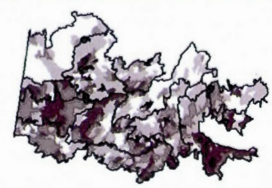
i. *Abies balsamea* in *Populus tremuloides* stands (basal area maximum value: 7%) (PotrF_abba)

j. *Abies balsamea* in *Picea mariana* stands (basal area maximum value: 25%) (PimaF_abba)

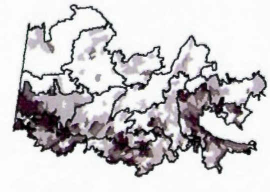


k. *Abies balsamea* stands (AbbaF)

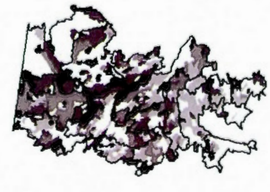
Increase of young *Picea mariana* and *Pinus banksiana* stands



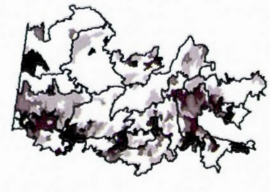
l. *Picea mariana* stands from the period centered on 1921 (PimaF_1921)



m. *Picea mariana* stands from the period centered on 1951 (PimaF_1951)

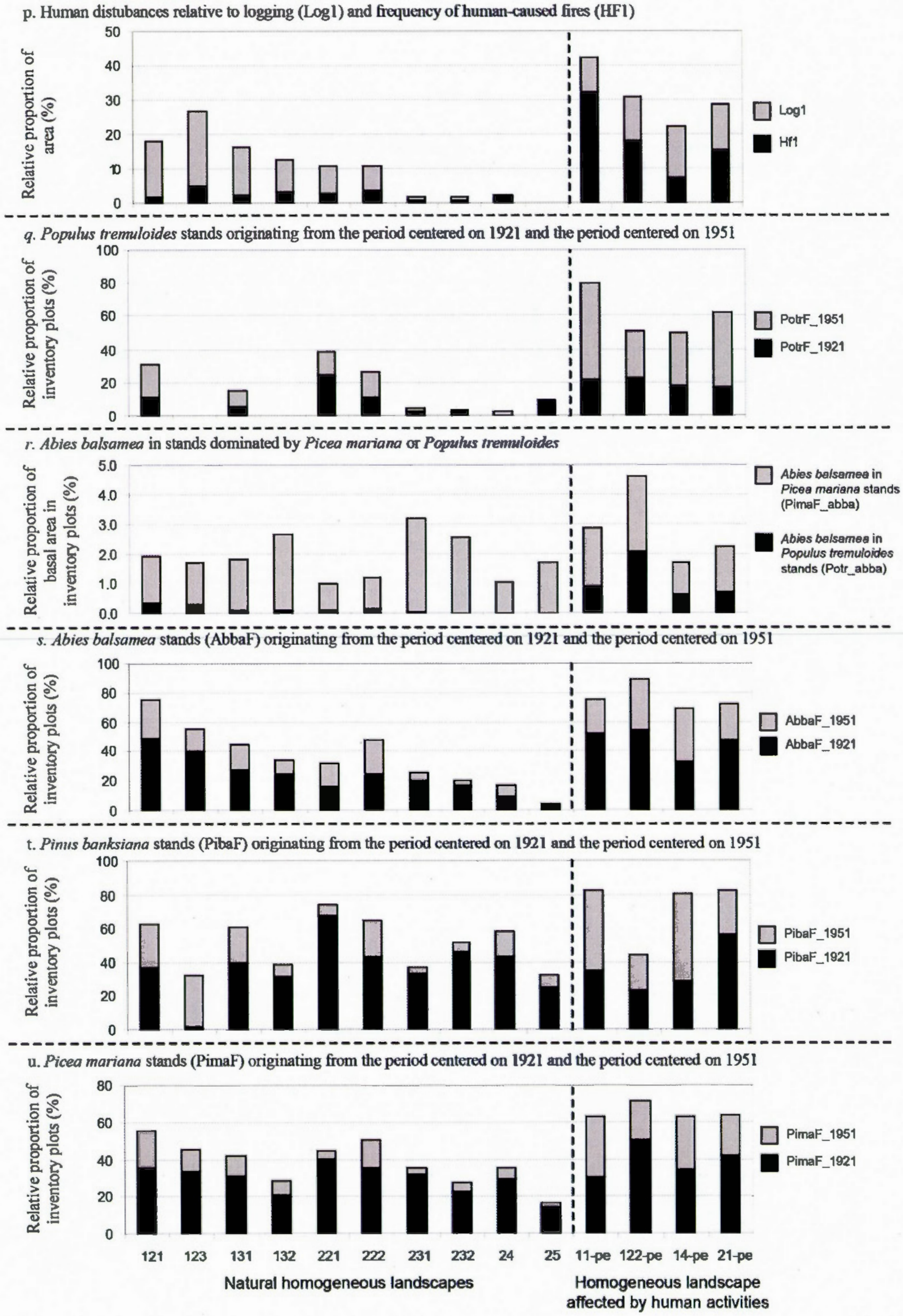


n. *Pinus banksiana* stands from the period centered on 1921 (PibaF_1921)

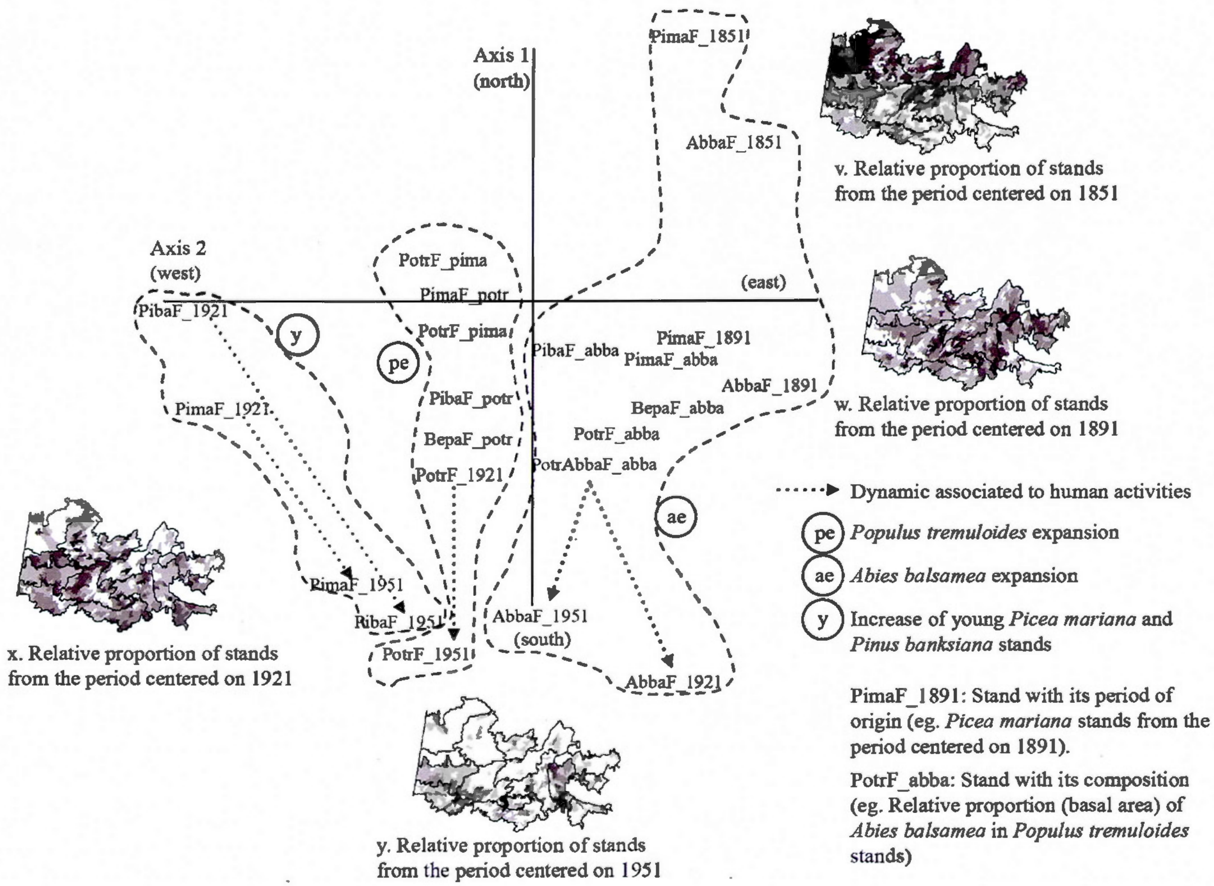


o. *Pinus banksiana* stands from the period centered on 1951 (PibaF_1951)

Appendix 6 (continued). Comparison between natural homogeneous landscape units and those affected by human activities



Appendix 6 (continued 2). Ordination diagram showing that forest types from the period centered on 1951 (after 1930) are concentrated in the southern portion of the territory and affected by human activities



APPENDIX 7

RECENT HISTORY OF HUMAN ACTIVITIES IN THE WESTERN PORTION OF THE STUDY AREA (ABITIBI)

This appendix consists of additional information supporting the hypothesis that the Abitibi clay belt (western part of the study area) was segmented into homogeneous landscape units (221 and 21-pe, Fig. 2.7A) by human activities related mainly to the agricultural colonization that took place between approximately 1870 and 1940. This hypothesis relies on a series of maps showing the relationship between current vegetation (Appendices 7a to 7c), natural sets of explanatory variables (Appendices 7d to 7f), and the increase of *Populus tremuloides* in homogeneous landscape units affected by human activities (Appendix 7h to 7j). On black and white maps, the darker the gray, the greater the proportion of the variable. On colored maps, colors and codes describe geographical units of natural (Appendices 7d to 7f) and human (Appendix 7i) sets of explanatory variables. The explanatory variables are defined in Appendix 2. On all maps, the homogeneous landscape units defined in Figure 2.7A are outlined in black. Appendices 7d to 7f were developed using a *K*-means clustering performed on data specific to each set of explanatory variables. The ecological structure of the Abitibi region consists of three main sections:

1- the southern portion possesses well-represented *Betula papyrifera* stands (Appendix 7a), a relatively mild climate (C2, Appendix 7d), stands that were the most affected by insect outbreaks, which occurred mainly during the period centered on 1921 (ND1, Appendix 7e), an undulated topography (28m in absolute difference of topographic elevation - Ele) with a predominantly very low slope (P_a : 70%), and an altitude of nearly 315m (PE5, Appendix 7f);

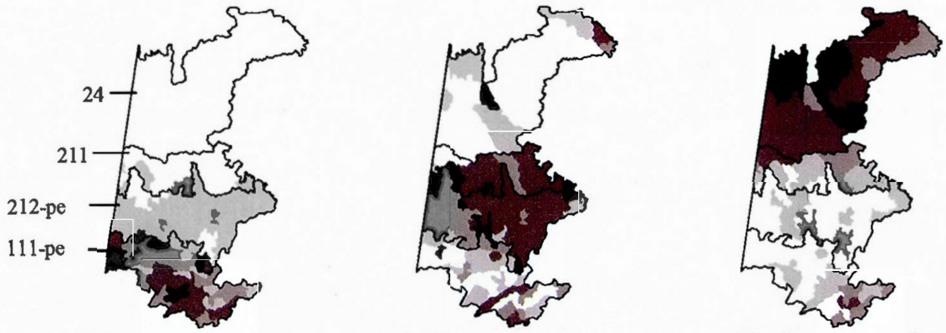
2- the central portion, which has an abundance of *Pinus banksiana* (Appendix 7b), a slightly colder climate (C5, Appendix 7d), a dominance of stands originating from fires of the period centered on 1921 (1921f) (ND4, Appendix 7e), a flat topography (Ele : 21m, P_a : 85%) (PE6, Appendix 7f), and an abundance of clay (Appendix 7g); and

3- the northern portion, which has a high proportion of wetlands (Appendix 7c), a colder climate (C8, Appendix 7d), a dominance of stands originating from the period centered on 1851 (prior to 1870) (ND7, Appendix 7e), and a very flat topography (Ele : 11m, P_a : 93%) (PE7, Appendix 7f).

This natural framework has been modified by human disturbances, which led to the subdivision of the central portion of the clay belt. From a uniform template (C5, ND4, PE6), two types of geographical units have been created: those affected by human activities, HD1, HD2, and HD5, and another that has remained in a relatively natural state: HD6 (Appendices 7i, 7j). These units differ markedly in regard to the proportion of *Populus tremuloides* stands (Appendix 7h), *Populus tremuloides* stands originating from the period centered on 1951 (Appendices 6d, 7j), logging recorded during the first survey program of the Ministère des ressources naturelles du Québec (MRN) (Log1, Appendices 6b, 7j), human fire frequency (Hf1, Appendices 6a, 7j), and agricultural activities (Fa1, Ag1, Ag2) (Appendix 7k). The overlap of all these variables supports the hypothesis that the Abitibi clay belt has been segmented into a southern homogeneous landscape unit affected by human activities (21-pe) and a northern landscape, which remains natural (221). Consequently, considering human disturbances while constructing an ecological land classification provides a clearer understanding of the impact of these activities on the heterogeneity of the study area and allows ecosystem management issues to be identified.

Appendix 7. Recent history of human activities in the western portion of the study area (Abitibi)

Vegetation

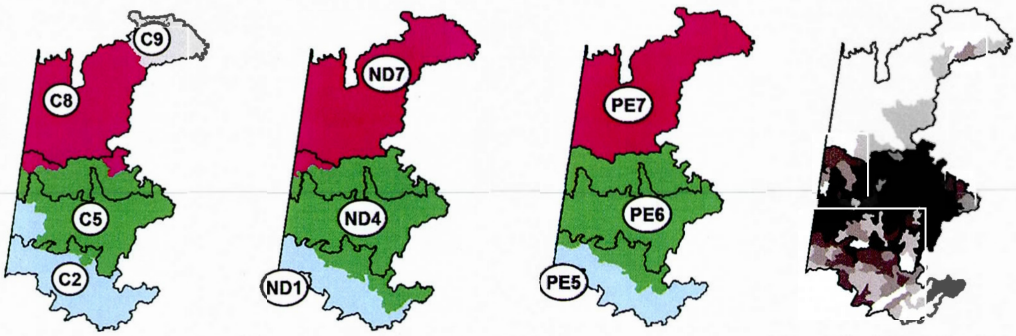


a. *Betula papyrifera* stands (BepaF, BepaAbbaF, BepaPimaF)

b. *Pinus banksiana* stands (PibaF)

c. Non forested wetlands (Wetland)

Natural sets of explanatory variables



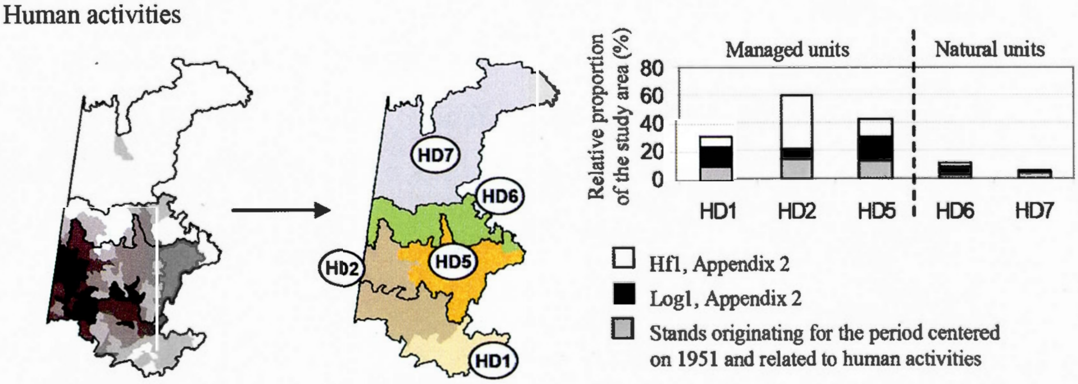
d. Climate (C)

e. Natural disturbances (ND)

f. Physical environment (PE)

g. Glaciolacustrine fine-textured (clay) surficial deposits (D_4ga)

Human activities



h. *Populus tremuloides* stands (PotrF, PotrAbbaF, PotrPimaF)

i. Human disturbances

j. Comparison of managed and natural geographical units

Appendix 7 (continued). Recent history of human activities in the western portion of the study area (Abitibi)

k. Description of the geographical units of sets of explanatory variables used to illustrate the effect of human activities in the western part of the study area.

Codes and description of variables are presented in Appendix 2.

		Physiography						Surficial deposits									Other
Physical environment	Unit	Malt	S_a	S_b	S_c	S_d	Ele	D_1a	D_1ar	D_2a	D_2b	D_4ga	D_4gs	D_7	D_wa	D_r	L_100km2
	PE7	242	93	5	1	1	11	2	1	0	0	6	0	63	7	3	0.8
	PE6	300	85	11	3	1	21	5	7	1	0	52	5	19	6	4	0.4
	PE5	314	70	17	9	3	28	19	13	2	0	26	9	14	9	8	0.6

		Spruce budworm outbreaks						Fires					Other
Natural disturbances	Unit	Sbon	Sbom	Sbos	1921o	1891o	1851o	Fia	Fif	1921f	1891f	1851f	Wi
	ND7	1	0	0	1	1	4	6	1	14	11	43	0
	ND4	5	3	1	11	4	7	4	1	33	15	18	1
	ND1	19	20	2	26	11	11	4	1	17	11	9	0

		Aridity regime			Thermal regime				
Climate	Unit	Preci	Vpd	Ari	Gdd	Mat	Dwf	Dwfc	Ef
	C9	309	1165	1.5	1069	-1.4	163	85	241
	C8	296	1287	1.8	1142	-0.5	165	85	240
	C5	319	1312	1.6	1258	0.4	173	92	246
	C2	302	1386	2.1	1349	1.1	175	95	249

		Logging			Fires		Agriculture		
Human disturbances	Unit	1951	Log1	Log2	Hf2	Hf1	Fa1	Ag1	Ag2
	HD1	9	15	14	13	7	0	1	0
	HD2	15	7	8	67	39	4	6	5
	HD5	13	17	29	7	13	1	2	1
	HD6	3	6	27	10	3	0	0	0
	HD7	4	1	4	3	1	0	0	0

APPENDIX 8

ADDITIONAL INFORMATION ON THE VEGETATION VARIATION EXPLAINED BY FOUR SETS OF EXPLANATORY VARIABLES (CLIMATE, NATURAL DISTURBANCES, PHYSICAL ENVIRONMENT, AND HUMAN DISTURBANCES) IN THE ENTIRE AREA AND THREE OF ITS PORTIONS

This appendix consists of additional information on variation partitioning. Variation partitioning analysis allows hypotheses concerning the origin of the landscape heterogeneity to be tested. Variation partitioning quantifies the relative contribution of sets of explanatory variables to vegetation changes occurring along the ecological gradients characterizing a study area (Borcard et al. 1992; Legendre et al. 2005; Tuomisto and Ruokolainen 2006, Legendre and Legendre 2012). In this study, variation partitioning is based on an RDA (redundancy analysis) of the species and a sites raw-data table. The variation partitioning analysis was performed initially, on the entire study area and, subsequently, on some parts of it.

The variation of vegetation is first split into two portions: explained variation and unexplained variation. The explained variation (corresponding to 100%) is divided into a proportion of variation related to unique sets of explanatory variables (e.g. only physical environment, PEu) and a proportion of variation common to several sets (physical environment and other sets of explanatory variables, e.g. PEc). Unique variation is a measure of the independence of a set in the face of changes in the other sets. An example of unique variation would be a set of natural disturbance variables (e.g. 1921f) that remain unchanged throughout a large territory (e.g. central portion of the study area), while other sets (ex. physical environment) show changes. Common variation is a quantitative measure of changes in vegetation closely related to simultaneous changes in several sets. When four sets of explanatory variables are considered, the total explained variation is partitioned into 15 fractions (e.g. PE∩C). The common double variation by a set is the sum of the double fractions containing this set (e.g. double common fraction of the set C = PE∩C + C∩ND + C∩HD). The common triple variation by a set is the sum of the triple fractions containing this set (e.g. triple common fraction of the set C = PE∩C∩ND + PE∩HD∩C + HD∩ND∩C). The common relative variation by a set is the sum of double, triple, and quadruple fractions containing this set (e.g. PEc = sum of PE∩C, PE∩HD, PE∩ND, PE∩C∩ND, PE∩HD∩C, PE∩HD∩ND and PE∩HD∩ND∩C) (7 fractions). The total relative variation by a set is the sum of unique and common fractions (e.g. PEt = PEu + PEc) (8 fractions). A fraction may be negative. This indicates that there is no linear correlation between Y (vegetation) and one of the explanatory variables (Legendre et Legendre 2012).

The entire area

Variation partitioning performed on the entire area shows that the vegetation variation explained by sets of explanatory variables (total variation: 65%) is higher than the unexplained variation. This indicates that changes in vegetation along ecological gradients are synchronized with those occurring in sets of explanatory variables. This result also allows us to characterize the landscape heterogeneity of the study area as structured or organized by specific links between vegetation and environmental variables.

Vegetation changes are mainly explained by combinations of the set of natural disturbances and other sets (e.g. NDc). The vegetation variation common to various combinations of sets is mainly defined by two triple combinations: PE∩C∩ND (13%) and HD∩ND∩C (12%), and the quadruple combination PE∩HD∩ND∩C (7.5%). The first triple combination characterizes the relationship between vegetation and natural sets (e.g. *Abies balsamea* species and spruce budworm outbreak). The second triple combination and the quadruple combination describe the relationship between the vegetation developed under the influence of anthropogenic activities (e.g. *Populus* *tremuloides* expansion), natural disturbances (e.g. spruce budworm outbreaks), climate (e.g. number of annual growing degree-days), and some elements of the physical environment (e.g. increase in peatlands from the south to the north). Finally, triple and quadruple combinations explain a greater variation of vegetation (33%) than double combinations (26%).

The variation explained by unique sets is mainly attributable to natural disturbances (NDu, 27%). This fraction shows a certain independence from natural disturbances, with variations occurring in other sets. The independence of vegetation from the set of natural disturbances is a constant in the study area (from the south to the north).

- In the southern part, the area covered by light spruce budworm outbreaks (Sbom, Appendix 5c) extends throughout the entire portion, although the southeastern portion is dominated by hilly topography and thick till, and the southwestern portion is mainly characterized by clay and undulating to flat topography (Appendix 5d).

- In the central portion, fires of the period centered on 1921 (1921f) play a leading role (from west to east, Appendices 5c, 6x).

- In the northern part, fires of the period centered on 1851 (1851f) are well-represented along the longitudinal gradient (Appendices 5c, 6v).

The *Abies balsamea* and *Betula papyrifera* domain

The results of the variation partitioning analysis carried out on this domain are similar to those for the entire area, although climate explained a smaller variation in vegetation. Given that the *Abies balsamea* and *Betula papyrifera* domain is relatively small and homogeneous, climate change (Cc, Ct) contributes less to explaining changes in the vegetation. In addition, the variation explained by the triple combination HD∩ND∩C (5%) is lower than that observed over the entire area. This was attributed to small variations along environmental gradients characterizing the *Abies balsamea-Betula papyrifera* domain with regard to these three variables. For example, insect outbreaks are relatively uniform (Sbom, Appendix 5c), as are logging (Log1, Appendix 6b) and climate (Gdd, Appendix 5b).

The *Picea mariana*-feathermoss domain

The results of the partitioning carried out in the *Picea mariana*-feathermoss domain differ from those of the previous areas, mostly by a decrease of variation partitioning explained by the combination of natural disturbances with other sets (NDc), in favor of a high unique fraction of natural disturbances (NDu). Of all the analyses performed on the variation partitioning of the vegetation (Grondin et al. 2007), this is the highest score on unique variation for a set of explanatory variables (40%). This result indicates the greater independence of natural disturbances from changes in other sets. This strong unique fraction is due to the relatively high proportion of stands of the period centered on 1851 (1851f) in the northern homogeneous landscape units of the *Picea mariana*-feathermoss domain (Appendices 5c, 6v) and to the strong representation of stands of the period centered on 1921 (1921f) in the southern part of this domain (Appendices 5c, 6x). Furthermore, human disturbances do not constitute an important set, which is consistent with the low impact of human activities in the *Picea mariana*-feathermoss domain.

The western portion (Abitibi)

The variation partitioning of this area is characterized by strong changes in vegetation and in all the sets of explanatory variables, including human disturbances, from the southwest to the northwest (Appendices 6 and 7). The explained vegetation variation reaches a value unequaled elsewhere (77%). Although natural disturbances, in combination with other sets (NDc, 79%), constitute the dominant set, all other sets (PEc, Cc, HDc) have high common fractions (50-55%). Triple and quadruple common fractions (47%) explain a variation clearly superior to that associated with double common fractions (25%). The quadruple combination (PE∩HD∩ND∩C) explains a high percentage of vegetation variation (21%). This result indicates a gradual increase (organic soils, forest stands of the period centered on 1851) or decrease (forest stands of the period centered on 1951-human activities, relative proportion of clay, forest stands of the period centered on 1921, annual number of growing degree-days) for all sets of explanatory variables from the south to the north in the western portion of the study area. The unique variation associated with human disturbance is lower than in other areas, but is still relatively high (21%). This indicates that some elements of natural disturbances are independent of changes in other sets. For example, the proportion of fires in the period centered on 1921 was near 15-20% in the southern part (11-pe) and in the northern part (25) despite significant changes in other sets.

Appendix 8. Detailed view of the relative proportion of vegetation variation (%) explained by 4 sets of variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to the entire study area and three of its portions.

	Entire area	Portion of the study area		
		***Abies balsamea - Betula papyrifera* domain**	***Picea mariana*-- feathermoss domain**	**Western portion**
Total variation				
Explained	65.0	58.6	62.5	77.6
Unexplained	35.0	41.4	37.5	22.4
Relative proportion of explained variation (15 fractions)				
Unique variation				
Cu	2.6	5.5	1.7	0.7
NDu	26.9	28.6	40.0	21.3
PEu	6.7	5.1	10.2	3.7
HDu	4.1	4.5	4.4	2.3
Common variation				
PE∩ND	9.4	8.7	7.5	3.7
PE∩C	2.7	2.0	6.0	3.3
C∩ND	5.6	4.3	5.6	5.1
PE∩C∩ND	13.0	11.1	8.2	10.9
PE∩HD	2.2	0.9	1.8	4.0
C∩HD	1.4	0.6	1.1	2.1
HD∩ND	5.1	9.3	4.1	7.0
HD∩ND∩C	11.7	4.6	7.6	7.8
PE∩HD∩C	1.0	2.2	0.9	4.6
PE∩HD∩ND	0.0	5.2	-3.1	2.5
PE∩HD∩ND∩C	7.5	7.4	4.3	21.0
	100	100	100	100
Sums of relative proportions of explained variation				
Total unique relative variation	40.4	43.6	56.2	28.0
Total common relative variation	59.6	56.4	43.8	72.0
Total relative variation by set				
PEt	42.5	42.6	35.6	53.6
Ct	45.5	37.8	35.2	55.4
NDt	79.4	79.2	74.1	79.3
HDt	33.0	34.8	21.0	51.4
Common relative variation by set				
PEc	35.7	37.5	25.5	49.9
Cc	42.9	32.3	33.5	54.7
NDc	52.4	50.6	34.1	58.0
HDc	28.9	30.3	16.5	49.0
Double common variation	26.4	25.9	26.0	25.2
Triple and quadruple variation	33.2	30.5	17.8	46.8

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CHAPITRE III

COMPARISON OF NATURAL AND MANAGED LANDSCAPES, AND REFERENCE CONDITIONS FOR ECOSYSTEM MANAGEMENT IN A LARGE PORTION OF THE EASTERN CANADIAN BOREAL FOREST

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Sera soumis à *Forest ecology and management*

3.1 Résumé

La comparaison des paysages naturels et des paysages aménagés, l'identification des unités se situant à l'extérieur des limites de variabilité naturelle et le développement de stratégies de restauration constituent les fondements de la mise en œuvre de l'aménagement écosystémique. L'intérêt de cette recherche est de modéliser les paysages naturels d'un vaste territoire de la forêt boréale canadienne (175 000 km^2), localement affectés par près d'un siècle d'activités anthropiques (exploitation forestière, incendies d'origine humaine), avec comme objectifs d'identifier les paysages aménagés qui excèdent les limites de leur variabilité naturelle. Une approche considérant le cycle de feu, la structure d'âge et la dynamique forestière est proposée pour décrire le paysage naturel de chacune des 14 unités homogènes de végétation qui composent la zone d'étude. Dans un premier temps, nous caractérisons la structure d'âge du paysage relativement à trois cycles de feu contemporains (110, 140 et 180 ans). Dans un deuxième temps, nous modélisons la dynamique forestière des 14 unités homogènes selon 20 combinaisons de végétations potentielles (5 types) et de stades de succession (4 types). Enfin, nous comparons la structure d'âge et la composition forestière de chaque unité homogène modélisée à celles des unités homogènes actuelles. Les analyses mettent en évidence quatre types géographiques de changements dans la composition de la végétation. Le type le plus important caractérise 5 unités homogènes situées dans la partie sud de la zone d'étude et il est principalement associé à la végétation potentielle de la sapinière à bouleau blanc. L'influence des activités humaines se traduit par une forte augmentation du peuplier faux-tremble et du bouleau blanc (stades de début de succession) et une diminution de la proportion de forêts plus de 100 ans (structure d'âge). Ces 5 unités sont considérées en dehors de leur variabilité naturelle, mais on estime que la majorité demeurent résilientes. Des stratégies d'aménagement visant à limiter l'enfeuillement et à augmenter la proportion de forêts de plus de 100 ans doivent être développées. À notre connaissance, il s'agit de la première étude comparative de paysages naturels et de paysages aménagés à couvrir une superficie aussi vaste et diversifiée et à être basée sur des processus naturels (cycle de feu, dynamique forestière). Les paysages naturels et leur variabilité plurimillenaire peuvent être considérés comme des états de référence pour l'implantation de l'aménagement écosystémique. La méthode développée pourrait être appliquée à d'autres territoires de la forêt boréale.

Mots-clés : aménagement écosystémique; dynamique forestière modélisée; unité homogène de végétation; végétation potentielle; cycle de feu; variabilité spatiale et temporelle

3.2 Abstract

The comparison of natural and managed landscapes, the identification of units outside of their natural range of variability and the development of restoration strategies are key elements of ecosystem-based management. This study models the natural landscapes of a vast area of the Canadian boreal forest (175,000 km2), locally affected by nearly a century of human activities (logging, human-induced fires), in order to identify managed landscapes that exceed the limits of their natural variability. Using an analytical framework that combines fire cycles, age structure and forest dynamics, we describe the natural landscape of the study area's 14 homogeneous landscape units. First, we characterize the landscape age structure relative to three contemporary fire cycles (110, 140, and 180 years). Second, we model the forest dynamics of the 14 homogenous units according to forest composition based on 20 combinations of potential vegetations types (5 levels) and successional stages (4 levels). Finally, we compare the age structure and forest composition of each modeled natural landscape to those of contemporary landscapes. Analysis reveals four types of geographically distinct forest composition. The predominant type characterizes 5 homogenous units located in the southern part of the study area and is associated mainly to *Abies-Betula* potential vegetation. The influence of human activities is reflected in a strong increase of *Populus tremuloides* and *Betula papyrifera* (early-successional stages) and a decrease in the proportion of forests more than 100 years old (age structure). These 5 units are considered to be outside of their natural range of variability, but the majority appear to have remained

resilient. Management strategies should aim to limit hardwood expansion and increase the proportion of forests over 100 years old. This is the first study comparing natural processes (fire cycles, forest dynamics) in natural and managed landscapes over such a large and diversified area. Application of this approach to other areas of the boreal forest would contribute to improved management of these areas. These natural landscapes and their millenial variability can be considered as reference conditions for the implementation of ecosystem-based management.

Keywords : Ecosystem-based management; forest dynamics modelling; homogeneous landscape unit; potential vegetation type; fire cycle, spatial and temporal variability

3.3 Introduction

Forest ecosystems are spatially heterogeneous and reflect ecological gradients that can be described according to vegetation and explanatory variables, such as climate, physical environment, natural and human disturbances (White, 1979; Legendre and Fortin, 1989; Wagner and Fortin, 2005). These gradients can be used to delineate homogeneous landscapes units (Rowe, 1962; Barnes et al., 1982; Bailey 1984; Grondin et al., 2007, 2014) and each of them can be described according to attributes such as fire cycle, age structure, and forest dynamics (White et al., 1999; Payette, 1992, 2010; Gauthier et al., 2001). In a homogeneous landscape unit characterized by a relatively short fire cycle (< 150 years), relatively flat topography and fairly dry climate, as in the western part of Quebec's boreal forest, 40 to 50% of forests are 100 or more years old (Bergeron and Fenton, 2012). In units with a hilly topography, rather humid climate, and relatively long fire cycle (> 500 years), such as in eastern Quebec, the proportion of forests over 100 years old can exceed 75% (Gauthier et al., 2008; Cyr et al., 2009; Grondin et al., 2010; Boucher et al., 2011).

Natural landscape and forest dynamics are closely related to fire (Payette, 1992). Following a fire, early-successional stages, such as *Betula papyrifera* stands, abound in homogeneous landscape units characterized by a relatively short fire cycle.

Inversely, late-successional stages, such as *Abies balsamea* stands, are well-represented in landscapes with longer fire cycles (Saucier et al., 2009). In both types of landscapes, early-successional stages can evolve towards late-successional stages in the absence of fire (Damman, 1964; Bergeron, 2000; Gauthier et al., 2010; Couillard et al., 2012). In the boreal forest of eastern Canada, *Betula papyrifera* and *Abies balsamea,* complemented by *Populus tremuloides* and *Picea glauca,* form a species assemblage with similar requirements in terms of climate, physical environment, soil nutrients and natural disturbances (Cogbill, 1985; Bergeron and Dubuc, 1989; Bergeron, 2000; Lesieur et al., 2002). This group of species with varying shade tolerance can form diverse types of forest stands or patches, grouped within a habitat type (Daubenmire 1968) or a potential vegetation (Powell, 2000). Potential vegetation (potential natural vegetation- PNV) is an internationally recognized (Powell, 2000; Ohmann et al., 2007), although sometimes controversial concept (Chiarucci et al., 2010). Two elements challenge this concept. The first is the occurrence of repeated and severe natural disturbances (fires, insect outbreaks) that can lead to a change in forest dynamics (alternative stable state) (Scheffer and Carpenter, 2003; Beisner et al., 2003; Jasinski and Payette, 2005). The second is the occurrence of repeated and severe human disturbances. For example, logging and human induced fires in some temperate regions that are naturally occupied by *Tsuga canadensis* and *Pinus strobus,* have facilitated the regeneration and development of broadleaf species and initiated an alternative type of potential vegetation (Mladenoff and Stearns, 1993; Laflamme, 2012). Consequently, some authors have argued that the use of the potential vegetation concept in countries that have been affected by human activities for a long time may not reflect natural conditions (Boucher et al., 2006). For our study area, we consider the use of the concept to be appropriate.We believe that human activities have altered the forest dynamics, notably through a significant increase in early successional stages. This increase took place without affecting ecosystem resilience. Ultimately, contemporary spatial variability can be defined in regard to two main levels or scales of observation: the homogeneous landscape unit (regional scale) and the potential vegetation-successional stage (local scale).

Forest ecosystems also show a temporal variability in both the short (200-300 years) and long term (several millennia). Each period has specific attributes in terms of climate, natural disturbances and forest composition (Carcaillet and Richard, 2000; Carcaillet et al., 2001; Ali et al., 2012, 2008; Cyr et al., 2009). Throughout the eastern boreal forest of North America, estimated fire cycles were less than 130 years during the Little Ice Age (LIA, 1450-1850), 230 years from 1850 to 1920, and are currently over 520 years (Bergeron 1991; Bergeron and Dansereau, 1993; Bergeron et al., 2001). Global warming since the end of the Little Ice Age may have created a climate less conducive to large forest fires (Bergeron et al., 2001), partly because of a thicker snow cover (Payette and Filion, 1985), which limits spring fires (Ali et al., 2008). The Holocene is mainly characterized by three periods. The first extends from 8000 to 4000 years BP (Holocene optimum). The climate, relatively warm and rainy, encouraged the growth of thermophilic species such as *Pinus strobus* in the current *Abies balsamea-Betula papyrifera* domain. Fires were relatively rare and late-successional species, such as *Abies balsamea,* abounded in landscapes. The Holocene climatic optimum was followed by the Neoglacial period, with the first portion (about 4000-2000 years) being characterized by a relatively cool climate. Rainfall increased slightly while summers where marked with droughts and fires (Carcaillet and Richard, 2000; Carcaillet et al., 2001). *Betula papyrifera* dominated the landscape. For about 2,000 years, and in some regions more recently, an increase in *Picea mariana* and *Pinus banksiana* is observed. This borealisation characterizes both bioclimatic domains studied (Garralla and Gajewski 1992; Richard 1980; 1993; Carcaillet et al, 2010).

Ultimately, all these environmental variations in space and time define the range of natural variability of landscapes (Landres et al., 1999). Gradually, over the last 50-100 years, human activities (especially logging) have modified the landscapes of Quebec's boreal forest, and the differences between natural and managed landscapes have widened. The proportion of forests over 100 years old has dropped drastically in some regions (Cyr et al., 2009). Natural patchiness has been homogenized and early-successional stands have increased significantly (Foster et al., 1998; Cogbill et al., 2002; Lorimer, 2001; Grondin and Cimon, 2003; Schulte et al., 2007; Laquerre et al., 2009; Boucher et al., 2009; Arbour and Bergeron, 2011). Among the tools used to reconstruct the original landscape in order to compare natural and managed landscapes are notary archives (timber sales) (Bouchard and Domon, 1997), surveyors' precolonial observations of forest composition (Dupuis et al., 2011), historical vegetation maps (Boucher et al., 2009) and models based on a combination of fire cycle, age structure and forest dynamics (Bergeron and Dansereau, 1993; Leduc et al., 1995; Gauthier et al., 1996, 1998; Harvey et al., 2002; Grondin et al., 2010). Natural and managed landscapes have been compared on the basis of large landscapes (e.g. grid of 25-km^2, Dupuis et al., 2011) or by considering environmental variables such as the altitudinal gradient (Vadeboncoeur et al., 2012). Only a few studies have focused on ecological classification (e.g. Harvey et al., 2002; Aubé, 2008).

Conceptually, this study falls into the field of landscape ecology (Turner, 2005); in practice, it relates to ecosystem management specifically in Quebec (Gauthier et al., 2008). Our goals are to 1) model the vegetation and the age structure of the natural landscapes of a vast territory (175 000 km^2) locally affected by nearly a century of human activities (logging, human induced fires), 2) identify the managed landscapes outside of their natural range of variability and 3) propose references conditions for implementation of ecosystem-based management.

3.4 Materials and methods

3.4.1 Study area

The study area covers nearly 175,000 km^2 of the eastern Canadian boreal forest. According to the hierarchical system of ecological classification used by the *Ministère des ressources naturelles du Québec* (MRN; Quebec Ministry of Natural Resources), this territory belongs to the boreal biome, specifically the *Abies balsamea–Betula papyrifera* domain in the south and the *Picea mariana*–feathermoss domain in the north (Saucier et al., 2009, Figure 1). Six of the tree species most common to this biome are well represented in both domains. Three are shade-tolerant (*Picea mariana* (Mill.) BSP., *Abies balsamea* (L.) Mill., and *Picea glauca* (Moench) Voss), and three are light-demanding (*Pinus banksiana* Lamb., *Betula papyrifera* Marsh., and *Populus tremuloides* Mich).

Ecological gradients characterizing the study area have been used to delineate 14 homogeneous landscapes, each considered as a portion of land with specific characteristics in terms of vegetation, climate, physical environment and disturbances (natural and human) (Figure 3.2). In the landscapes of the southern portion, *Betula papyrifera*, *Picea mariana,* and *Abies balsamea* are abundant. The topography is generally hilly. Both fires and spruce budworm outbreaks (*Choristoneura fumiferana* (Clemens) have occurred in the area (Table 3.1). In the landscapes of the central portion of the study region, *Betula papyrifera, Populus tremuloides, Picea mariana* and *Pinus banksiana* are abundant. *Abies balsamea* increases along the longitudinal gradient (from west to east). Natural disturbances were mainly associated to fires of 1921 period (Table 3.1). In the northern portion, *Picea mariana* is the most abundant species. Fires constituted the main natural disturbances and were more abundant during the 1851 period (< 1870) than in the 1921 period. The landscape in the northwestern extremity has a flat topography dominated by organic deposits; a considerable part of its forested area was affected by fires during the 1851 period (< 1870). Some landscapes located in the southern part show *Populus tremuloides* expansion caused by nearly 100 years of human activities. Most of the northern landscapes have also been affected by logging, but generally more recently (since 1970).

3.4.2 Characterization of the modeled natural landscapes

The natural landscape is qualified as modeled because it was created by the combination of the fire cycle, age structure and forest dynamics.The modeled natural landscapes were defined at the regional level on the basis of homogeneous landscape units and at the local level by forest composition (potential vegetation and successional stage). An overview of the approach used to define the natural landscape of each homogeneous unit is presented in Figure 3.3.

3.4.2.1 Fire cycle and age structure

Fire cycle and age structure are the first components essential to model natural landscapes (Bergeron and Dansereau, 1993; Leduc et al., 1995; Gauthier et al., 1996, 1998) (Figure 3.3A1, appendix A). The data required to define fire cycles were obtained from published fire origin maps (e.g. Bergeron et al., 2001, 2004) as well as from forest inventory plots produced by the MRN. Each plot of the forest inventory (MRN) with no evidence of human activity (n = 38 576) was attributed a year of origin determined by the age of the oldest tree, estimated by counting the annual rings of a core taken with a Pressler borer at the base of dominant trees (three trees per plot).

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We defined the fire cycle and age structure of each homogeneous landscape unit by the following steps.

1- We analyzed fire origin maps and their associated fire cycle for portions of 8 of the 14 homogeneous units making up the study area (Figure 3.4). These portions cover a total area of almost 40 000 km^2, representing 23% of the territory. The largest map (15 000 km^2) was produced by Bergeron et al. (2001) for the western end part of the study area (F1 to F4, Figure 3.4). We defined four periods of origin based on analysis of this map: 1851 (< 1870), 1891 (1870-1900), 1921 (1901-1930) and 1951 (> 1930).

2- We subdivided the fire origin map produced by Bergeron et al. (2001) according to the four homogeneous landscape units located in the western portion of the study area (Figure 3.4; 11-pe, 21-pe, 221, 25). For each of these landscapes, we determined the relative proportion of the four periods of origin defined above. We also characterized the forest inventory plots (MRN), located in each of the four homogeneous landscapes mapped by Bergeron et al. (2001), in regard to four periods of origin. We characterized the time since fire for each inventory plot in regard to four periods because plot age is not precise. We compared both distributions, and their similarity confirms the usefulness of the two data sources (fire origin maps and forest inventory plots) for estimating the fire cycle of each homogeneous landscape unit of the study area (Appendix A6).

3- Following Bergeron et al. (2001) and Payette (2010), we defined a fire cycle for each homogeneous landscape unit on the basis of available information (fire origin maps, forest inventory plots). The fire cycles are considered as the average age of the forest stands that developed after the last contemporary fire.

4- We grouped several adjacent homogeneous units with a similar fire cycle in order to define three spatial fire cycles. We also qualified each spatial fire cycle in terms of temporal natural variability by considering the fire cycle identified by previous fire origin maps or paleoecological data based on charcoals. The limits (lower and upper) correspond to the shorter and the longer fire cycles described by these authors (Figure 3.5, Appendix A1).

5- We estimated the age structure of each homogeneous unit based on the three spatial fire cycles (Van Wagner, 1978; Johnson and Van Wagner, 1985, Figure 3.3A2). This age structure allowed us to define the proportion of a landscape covered by each age class ranging from 10 to 500 years since the last fire.

3.4.2.2 Forest composition and forest dynamics

Forest composition and forest dynamics constitute the second components used to model the natural landscapes (Bergeron and Dansereau, 1993; Leduc et al., 1995; Gauthier et al., 1996, 1998) (Figure 3.3A1, appendix A). Forest dynamics reflect changes according to the mean time elapsed since the last fire. These two components were developed on the basis of potential vegetation types and their successional stages (Saucier et al., 2009). Five potential vegetation types reflect the diversity of forest vegetation observed in the study area : *Abies-Betula* (Ms2), *Picea-Populus*

(Me1), *Abies-Picea* (Rs2), *Picea*-mosses (Re2) and *Picea*-sphagnum (Re3). Each of these was divided into four successional stages defined by the relative proportion of shade tolerant forest species: early-successional (S2), intermediate (S3), facies (S4) and late-successional (S5) forests (Dansereau, 1957; Rey, 1960; Saucier et al., 1994). This classification is similar to the cohort system of Harvey et al. (2002).

To model the forest dynamics, we relied on the MRN's forest inventory plots and proceeded according to the following steps.

1- We characterized each forest inventory plot according to one of the 20 combinations of potential vegetation-successional stages. We used these plots, characterized by the combination of potential vegetation-successional stage and year of origin (see previous section), to define the relative frequency according to 10-year age classes and along a chronosequence extending from 30 to 500 years (Figure 3.3A3, Appendix B).

2- We adjusted the relative frequencies specific to each combination of potential vegetation-successional stage to the Weibull distribution to estimate the parameters (λ, σ, θ) subsequently used to model temporal forest dynamics. Equations were developed using R statistical language (R Development Core Team, 2010, library stats4) and a Kolmogorov-Smirnov test was used to confirm that the Weibull distribution adequately represented the relative frequency of plots (null hypothesis).

3- We based the integration of forest modeling and age structure for each of the 14 homogeneous landscape units on two weightings.

3.1- The first (Figure 3.3A4) integrated the structure defined by the Van Wagner distributions (Figure 3.3A2) and the forest dynamics modeled by the Weibull distribution at the level of the potential vegetation and the successional stage

(Figure 3.3A3). This procedure was extended to all successional stages for each potential vegetation type.

3.2- A second weighting (Figure 3.3A5) integrated the forest dynamics into each homogeneous landscape unit (e.g. HL : 121), considering the relative area occupied by each potential vegetation type in the unit (e.g. Ms2). These relative areas (e.g. Ms2- HL 121) were calculated using MRN forest maps (1990-2000, third decennial program), on which potential vegetation type was determined for each forest polygon based on photo-interpretation of aerial photographs.

4- To estimate the natural variability of forest composition for each homogeneous landscape, we applied the steps described above (3.1, 3.2) to shorter and longer fire cycle temporal variability (Figure 3.5, Appendix A1). The final result for each homogeneous unit shows the relative proportion of vegetation (potential vegetation-successional stage) accompanied by a minimum and maximum proportion, which correspond to the lowest and highest values of plurimillenial fire cycle variability (Figure 3.3C2). For example, the proportion of *Abies-Betula* late stages (Ms2-S4S5) in the HL 121 varies from close to 27 to 37 %, considering that the fire cycle of this homogeneous landscape shows a temporal fire cycle variation from 47 to 340 years.

3.4.3 Description of the managed landscape

1- We defined the managed landscape using the detailed MRN's forest maps (scale 1 : 20 000, third decennial program) (Figures 3.3B1, B2). Using these forest maps, each of the 14 homogeneous landscape units was characterized in regard to its structure. The age structure was described on the basis of histograms on which the structure was presented relative to four classes: 10 (1-20), 30-50 (21-60), 70-90 (61-100) and 120 (>100) years old (Figure 3.3C1). These ages correspond mainly to the time elapsed since the last fire, except for stands dominated by balsam fir whose ages indicates mainly a time elapsed since the last insect outbreak.

2- Using the forest maps, we characterized each of the 14 homogeneous landscape units in regard to its current or managed composition. Each polygon was characterized by a forest composition and a potential vegetation (photo-interpretation). A successional stage was attributed to each polygon on the forest maps. For example, the stands dominated by *Betula papyrifera* are referred to as S2 successional stage (early successional stage). Recent logging was considered as a specific class.

3.4.4 Comparison of natural and managed landscape

1- Modeled natural landscapes and managed landscapes were compared with respect to their age structure. The description of the age structure of the modeled natural landscape was derived from their fire cycle (Figure 3.3C1).

2- Modeled natural landscapes and managed landscapes were compared with respect to forest composition (potential vegetation and successional stage) (Figure 3.3C2). To facilitate the visual comparison of these two types of landscape, an ordination diagram resulting from a correspondence analysis (CA) was produced using R statistical language (R Development Core Team, 2010, vegan library). The data submitted to R concernerd the relative importance of each combination of potential vegetation-successional stage for the 14 homogeneous landscapes described in terms of natural and managed landscapes. The analysis of ordination led to the identification of landscape types.

3- The differences between natural and managed landscapes were calculated in order to evaluate the changes in age structure and composition. These differences were classified into five classes from very low (< 20%) to very high (> 80%). Homogeneous landscape units characterized by high differences and showing a current relative proportion of forest composition higher than natural landscapes (Figure 3.3C2) were considered to be outside of their natural range of variability. Results presented by Grondin et al. (2014), which describe the influence of human activities on forest dynamics, also helped determine which landscapes were outside of their natural range of variability.

3.5 Results

This section presents the modeled natural landscapes of a large portion of the Quebec boreal forest defined by an approach based on fire cycle, age structure, and forest dynamics (Figure 3.3).

3.5.1 Fire cycles and age structure of the natural landscape

Three distinct fire cycles characterizing the study area were determined on the basis of fire origin maps (Figures 3.4, 3.5, Appendix A) and forest inventory plots (MRN). These fire cycles were used to determine the age structure of each homogeneous landscape. The first brief fire cycle (110 years) was noted by Bergeron et al. (2001) and Le Goff et al. (2007) (Figure 3.4, F6-F7, Appendix A2b) in two homogeneous landscape units belonging to the *Picea mariana*-feathermoss domain (222 and 24). The rarity of *Abies balsamea* and the relatively high proportion of sandy deposits occupied by *Pinus banksiana* are evidence of this brief fire cycle. Based on the two studies mentioned above, we estimate that the temporal variability of this fire cycle extends from 56 to 315 years. According to the forest inventory plots, these two landscapes have a forest cycle close to 140 years (Figure 3.5). This relative long fire cycle may be explained by a number of causes, including the lack of inventory plots in areas that have burned recently. The addition of these plots would have the effect of reducing the fire cycle length.

The second fire cycle (140 years) characterizes the homogeneous landscape units of the southern part of the study area, which belong to the *Abies balsamea-Betula papyrifera* and the *Picea mariana*-feathermoss domains. This fire cycle is closely related to fire origin maps produced by Bergeron et al. (2001, Figure 3.4, F1 to F3) and Lesieur et al. (2002, F8). Four of the landscapes (123, 122-pe, 121, 221) are dominated by stands of the 1921 period, while the three others (11-pe, 14-pe and 21-pe) are slightly dominated by stands of the 1851 period (Table 3.1, Appendices A8, A9). In accordance with contemporary authors (Bergeron et al., 2001, 2004; Lesieur et al., 2002) and paleoecological studies (Carcaillet et al., 2010), we estimate that the natural variability extends from 47 to 340 years (Figure 3.5, Appendix A1). The fire cycle values prior to 1850 (the end of the Little Ice Age) presented by the previous authors are lower than those characterizing the 1850-1920 period.

The third fire cycle (180 years) characterizes homogeneous landscape units of the northern part of the study area, most belonging to the *Picea mariana*-feathermoss domain. On figure 3.5, landscape 132 is close to other units affected by the second fire cycle (fire cycle estimated by forest inventory plots). This landscape is associated with the third cycle for two main reasons. The first is the low proportion of *Pinus banksiana* and its abundance of *Abies balsamea.* The second is the proximity and similarity of landscape 132 to the region studied by Bélisle et al. (2011). This region is located in the eastern part of the *Picea mariana*-feathermoss domain and is characterized by a 247-year fire cycle. Homogeneous landscape units associated with this third fire cycle are characterized by a relatively high proportion of stands of the 1851 period (231, 232, 25). The difference between the proportion of stands originating from the 1851 period and those of the 1921 period is in the range of 15-20%, but reaches 50% for unit 25. This result, as well as the abundance of organic deposits (Table 3.1, Appendices A8, A9), suggests the presence of a fire cycle specific to this last landscape. However, considering the fire cycle reported by the authors (close to 170-180 years, Figure 3.5) and also with the aim of restricting the number of fire cycles, we preferred to classify landscape 25 in the third fire cycle. Natural variability ranges from 65 to 446 years (Figure 3.5). If we exclude the paleoecological value reported by Cyr et al. (2005, 446 years, F5, Figure 3.4), the variability of this longest fire cycle decreases from 446 to 310 years (Figure 3.5).

3.5.2 Forest composition and forest dynamics of the natural landscape

A specific forest composition and forest dynamic is associated to each potential vegetation type identified in the study area (Figure 3.6, Appendix B). The comparison of the 5 potential vegetations reveals a dominance of the early-successional stage (S2) for a period of about 60 to 80 years since the last fire. During this period, all successional stages are present in the landscape. Later, and for as long as about 110-130 years, all successional stages remain present, but mid-successional stages (S3-S4) dominate the landscapes. Diversity and heterogeneity are at their optimum (Shafi and Yarranton, 1973; Harper et al., 2002; Bergeron and Fenton, 2012). After 130-140 years, late-successional stands (S5) abound, and come to dominate the landscape after 200-250 years. Stands of successional stages S2, S3 and S4 gradually decrease in abundance and in successive waves. We consider that each potential vegetation has its own dynamics, regardless of the homogeneous landscape. For example, the *Abies-Picea* potential vegetation type has nearly the same forest dynamics in the *Abies balsamea-Betula papyrifera* domain as in the *Picea mariana* feathermoss domain.

3.5.3 Comparison of natural and managed landscapes

3.5.3.1 Four types of forest composition at the landscape level

The comparison of the natural and managed landscapes is presented through an ordination diagram (Figure 3.7) and histograms (Figures 3.8, 3.9). Elements complementing each other highlight four types of forest composition (TY1 to TY4), each characterized by a specific geographical distribution. On the first axis, the homogeneous landscape units are positioned from west (221) to east (122-pe) (Figure 3.2). Along this longitudinal gradient, both topographic elevation (Table 3.1) and relative abundance of *Abies-Betula* potential vegetation (Ms2) increase, while *Picea*-mosses (Re2), *Picea*-sphagnum (Re3), and *Picea-Populus* (ME1) potential vegetations decrease. On the second axis, landscapes are positioned relative to changes from natural to managed landscapes. Vectors are relatively long, indicating that changes between natural and managed states are wide ranging.

Among the 14 homogeneous landscapes, one has been selected to illustrate each of the four types of forest composition observed (121, 14-pe, 222, 231) (Figure 3.8). The first type (TY1) characterizes the homogeneous landscape located in the southern part of the *Abies balsamea-Betula papyrifera* domain (121, 11-pe, 122-pe, 123,

Figure 3.7b), and naturally dominated by late stages of *Abies-Betula* (Ms2-S4S5) (Figure 3.7A). In the managed landscapes, early stages of *Abies-Betula* (Ms2-S2S3) abound (Figure 3.8).

The second type of forest composition (TY2) is defined by units located in the northern part of the *Abies balsamea-Betula papyrifera* domain (14-pe, 131, 132). These landscapes are naturally dominated by the late-successional stages of both *Abies-Picea* (Rs2-S4S5) and *Picea*-mosses (Re2-S4S5) potential vegetations. Changes in forest composition are less notable than among other types (TY1,TY3,TY4), as confirmed by the short length of vectors (Figure 3.7). Landscape 132 has the shortest vector; suggesting a strong similarity between natural and managed landscapes (Appendix C1). All combinations of potential vegetation-successional stages decrease, mainly due to logging. Even if *Abies-Betula* potential vegetation is not dominant, the proportion of early stages (Ms2-S2S3) increases considerably from natural to managed landscape.

The third type of forest composition (TY3) is associated with landscapes located in the central and north-central portions of the study area (222, 232, 24). These landscapes belong to the *Picea mariana*-feathermoss domain and are naturally dominated by *Picea*-mosses late stages (Re2, S4-S5). The long vectors of the ordination diagram mainly reveal the major impact of recent logging (since 1970). Figure 3.8 shows that logging affected 15-20% of landscape 222. All combinations of potential vegetation-successional stages decrease. Late stages of *Picea*-mosses (Re2-S4S5) remain stable while we expected a slight decrease. This phenomenon is difficult to explain because the fire cycle, forest plots and forest maps considered in this study could all play a role, each having its own respective limitations.

The fourth type of forest composition (TY4) includes units in the north-western part of the study area (21-pe, 221, 231, 25). These landscapes belong to the *Picea* *mariana*-feathermoss domain and are naturally dominated by *Picea*-mosses potential vegetation (Re2) and sub-dominated by various potential vegetation types, including *Picea*-sphagnum (Re3). In some landscapes, the *Picea-Populus* vegetation type (ME1) is well represented. Changes from natural to managed landscapes are still quite notable, and mainly caused by recent logging. A small representation of early stages of *Picea*-sphagnum (Re3-S2S3) is observable in natural landscapes (7%), compared to a negligible presence of this combination (<1%) in managed landscapes.

3.5.3.2 Changes in forest composition specific to each potential vegetation

Regardless of the type of change in forest composition, each potential vegetation type exhibits a specific response to anthropogenic activities. The relative proportion of *Abies-Betula* early stages (Ms2-S2S3, pale blue color in Figure 3.8) increases significantly at all locations where it is well represented (TY1-TY2-TY3), but mainly where the first type of composition is evident (TY1).

The early stages of *Abies-Picea* (Rs2-S2S3, pale green color in Figure 3.8) never reach abundance covering less than 15% of natural landscapes. In the presence of all types of forest composition (TY1 to TY4), we observe a slight decrease of approximatively 5-10% from the natural modeled to the managed landscape. Late stages of *Abies-Picea* (Rs2-S4S5, dark green color on Figure 3.8) is generally a sub-dominant type of forest composition, except for forest composition TY2, where it is dominant. This combination decreases under the influence of human activities (logging). In managed landscapes, late stages of *Abies-Picea* (Rs2-S4S5) remain more abundant than early stages (Rs2-S2S3), which explains the former's higher position on the second axis of the ordination diagram (Figure 3.7A).

Picea-Populus potential vegetation (Me1, pale and dark yellow in Figure 3.8) is typical of landscapes 231, 221, and 21-pe (abundance of clay deposits, Table 3.1). Comparing natural and managed landscapes reveals few changes in landscape 231. Due to recent and intense logging (since 1980), we expected a significant increase in hardwood species in this landscape (Grondin and Cimon, 2003; Laquerre et al., 2009; Arbour and Bergeron, 2011). However, hardwood expansion took place in unit 21-pe, which has been affected by human activities for close to a century (Appendix C1, Chapter 2, Appendix 6).

The early stages of *Picea*-mosses (Re2-S2S3, pale orange color in Figure 3.8) are never a dominant combination and occupy a sub-dominant position compared to late stages of *Picea*-mosses (Re2-S4S5, dark orange color). In forest composition types TY3 and TY4, the abundance of early stages of *Picea*-mosses (Re2-S2S3) decreases by almost 10% from the natural to the managed landscape because of recent logging and fires. Late stages of *Picea*-mosses (Re2-S4S5) present two patterns of forest dynamics. In the first, typical of TY2, the proportion of area occupied by this combination (Re2-S4S5) decreases slightly (10%) because of logging (14-pe). In the second pattern, typical of TY3 and TY4, the proportion of late stages of *Picea*-mosses (Re2-S4S5) is similar in modeled and managed landscapes (121, 222, 231).

Picea-sphagnum potential vegetation (Re3, pale and dark pink in Figure 3.8) is observed primarily in the *Picea mariana* domain, where organic deposits are more abundant than in the *Abies balsamea-Betula papyrifera* domain (Table 3.1). The proportion of early-successional stages (*Larix laricina*) is generally low (5-10%) in the natural landscape and rare in managed ones. The long vectors characterizing landscape 25 (rare logging) result mainly from different proportions of early-successional stages in natural versus managed landscapes.

3.5.3.3 Summary of the main differences between natural and managed landscapes

The comparison of natural and managed landscapes on the basis of age structure and forest composition (Figure 3.9) reveals significant decreases in: 1) forest stands more than 100 years old and 2) late successional stages (S4S5) for all potential vegetation types. Five homogeneous landscape units are considered outside of their natural range of variability (Figure 3.9A, 3.9B, 3.9C) because they are strongly affected by forest logging followed by an increase in abundance of *Populus tremuloides* (Figure 3.9D, 3.9E). The main difference between natural and managed landscapes outside of their natural of variability is related to *Abies-Betula* potential vegetation (Ms2) (Figure 3.10). The difference is obvious for 11-pe, 121 and 122-pe, and more subtile for the two others principally characterized by a decrease in the late successionnal stages of *Abies-Betula*, but also *Populus-Picea* potential vegetations. Figures 3.9D and 3.9E clearly shows that a high proportion of logging and *Populus tremuloides* characterize homogeneous landscapes 14-pe and 21-pe (see laso chapter 2, appendix 6). Restoration of the landscapes highly managed should rely on landscape strategies based on natural landscapes. The natural landscapes of all the homogeneous landscapes of the study area, and their plurimillenial temporal variability, are presented in figure 3.11. The four geographical types of forest composition are clearly distinguished (TY1 to TY4). In each type, late successional stages (dark colors, S4S5) are more abundant than early successional stages ones (light colors, S2S3). Although millennium variability of fires is large (50-350 years, Figure 3.5), variability in forest composition remains low. The difference between 1) the mean relative proportion of area occupied by a specific combination of potential vegetation-successional stages and 2) the relative proportion of area reached by each extremes values of variability of this combination (the longest or the shortest), does not exceed 10%.

3.6 Discussion

The findings of this study parallel those of previous comparisons of natural and managed landscapes that evaluated the impact of human activities (e.g. Boucher et al., 2009) on the basis on an ecological classification (e.g. Harvey et al., 2002) in the goal of defining reference conditions (Boucher et al., 2011).

Fire cycle (spatial and temporal variability)

Three complementary approaches were used in this study to estimate contemporary spatial fire cycles (110-140-180 years). The approach that yields the most precise results considers fire origin maps developed by various authors (e.g. Bergeron et al., 2010), but these maps cover a limited portion of the study area. To characterize the 14 homogeneous landscapes units by a fire cycle we used, as a supporting source of information, the forest inventory plots of the MRN. The scope of these forest plots, mainly produced in young and mature forests (more than 30 years) has some limitations, such as not considering recently burned areas. Consequently, in some homogenous landscapes (e.g. 24), the fire cycle determined from maps was preferred instead, even if the map does not cover the total area of the homogeneous landscape unit.

A third approach to classifying homogeneous landscapes according to contemporary fire cycles focused on forest species. The link between *Pinus banksiana* and the fire cycle is typical of the boreal forest (e.g. Dix and Swan, 1971) and is obvious in the first (110 years, higher proportions of *Pinus banksiana*) and third (180 years, lower proportions) fire cycles (Appendix A7). This relationship is less clear in the second fire cycle (140 years), where *Pinus banksiana* is well represented in some landscapes (eg HL 131, 14-pe-pe 21, Figure 3.2) and rare in others (eg, 121, 123) (Appendix A7). These landscapes are also distributed in different ecological units (e.g. southern and northern portion of *Abies balsamea-Betula papyrifera* domain) according to our ecological land classification (Figure 3.2) and we were expecting a closer relationship between this classification, abundance of *Pinus banksiana* and fire cycles. To explain this phenomenon, Bergeron et al. (2004) estimated that fire severity and topography can create distinct types of forest landscape composition, even if the fire cycle is the same. The undulating hilly topography of the southern part of the study area is characterized by the sporadic presence of topographic refuges, considered to be less affected by fires and more favorable to the persistence of *Abies balsamea* than open areas (Grimm, 1984). In contrast, flat and gently undulating topography favors high severity fires and regeneration of *Pinus banksiana* (Rowe and Scoter, 1973). Analyses of the contemporary fire cycles at the local level of potential vegetation, complemented by paleoecological studies of sediment archives (lakes, peatlands, Ali et al., 2008, 2012) and charcoal obtained from mineral soils (Payette et al., 2012), are needed to improve our understanding of the relationships between the physical environment and natural disturbances.

We also examined the temporal variability of fire cycles according to three periods: the Holocene up to the Little Ice Age (1550), the LIA (1550-1850) and the post LIA period (1850-1920) (Bergeron et al., 2001; Lesieur et al., 2002; Le Goff et al., 2007; Richard, 1980, 1992; Carcaillet et al., 2010; Cyr et al., 2005; Bergeron and Fenton, 2012). We determined temporal variability based on the shortest and longest fire cycles characterizing the three periods mentionned above and the three spatial fire cycles (Figure 3.5). For all these fire cycles (110, 140, 180 years), the temporal natural variability is similar and extends from approximately 50 to 350 years (Figure 3.5). We estimated that our approach, which took into account a large part of the natural variability of fire cycles allows us to identify landscapes that are outside the range of their long-term variability with a higher degree of confidence. The longest temporal fire cycles characterize primarily the middle Holocene (climatic optimum), when vegetation was quite different from today. For example, the sites presently occupied by *Abies-Betula papyrifera* potential vegetation in the *Abies balsamea-Betula papyrifera* domain were occupied by *Abies-Betula alleghaniensis* potential vegetation (Richard, 1993). In the southern domain, *Pinus strobus* was also more abundant in the landscape than it is today.

Age structure

An age structure following a negative exponential was defined on the basis of contemporary fire cycles with the aim of evaluating the relative proportion of area occupied by age classes ranging from 30 to 500 years. This procedure has some limitations. Van Wagner (1978) demonstrated that, under certain conditions (Payette, 2010), the probability distribution of age in a landscape subject to periodic renewal by fire was exponential. Empirical studies have partially supported this hypothesis (Bergeron et al., 2001). Under typical boreal disturbance regimes, Boychuk and Perera (1997) estimated that forest age structure should not follow an exponential distribution, even at very large spatial scales, due to the distribution of disturbances. For example, fires in our study area mainly occurred around 1820 and 1910-20 (Bergeron et al., 2001); this distribution can be considered as exponential when fires are grouped in periods (e.g. 1851-1891-1921-1951). The exponential distribution is still less evident in regions with infrequent and large fires (Bouchard et al., 2008). In the study area, we estimated that the use of Van Wagner's (1978) probability distribution was the best way to define a theorical age structure. However, our age structures do not directly consider the effect of insect outbreaks in terms of both types in forest composition and age class (Boucher et al., 2011). Our approach is justified by the relatively high variability and low impact of insect outbreaks on the forest composition and age structure in the study area (Bouchard et al., 2007). The prevailing situation in boreal ecosystems differs from that of the temperate zone, where the impact of outbreaks is more extensive (Bouchard et al., 2007; Duchesne and Ouimet, 2008). Furthermore, the forest inventory plots and maps used in this study are themselves a reflection of past outbreaks. The impact of insect outbreaks is thus indirectly considered in our study.

Forest dynamics

We considered the forest dynamics at two levels of observation of an ecological land classification. At the regional level, we used the concept of homogeneous landscape units because it reflects the integration between vegetation and several sets of explanatory variables: climate, physical environment, natural and human disturbances. All these variables play a key role in determining the fire cycle, age structure, forest dynamics and modeled natural landscape. At the local level of observation, forest composition and forest dynamics have been described using five potential vegetation types because: 1) they constitute the foundation of the hierarchical system of ecological classification used in Québec (Saucier et al., 2009) and in many other countries (Bailey, 1984; Powell, 2000); 2) they allow us to conduct a comparative analysis of natural and managed landscape by taking into account forest types exhibiting the same dynamics (successional pathway) and 3) they are considered to be an interesting way to describe the study area on the basis of four geographical types of forest composition. The natural landscapes described on theses two level of perception (regional and local) are considered as reference conditions developed on the basis of processes that control the landscape heterogeneity (Figure 3.11). These reference conditions are different from those proposed by other authors (Boucher et al., 2011) in that the description is based on potential vegetation and successional stages, and also takes into account the Holocene temporal variability of fire cycles that extends mainly from 50 to 350 years. Even if this fire cycle variability is high, the change is forest composition showed limited variations (Figure 3.11). This indicates that Holocene vegetation changed as a result of climate and fire variabilities, but within a range that has always remained relatively narrow (Cyr et al., 2009).

Our findings demonstrate that human activities can strongly increase the proportion of early successional stages characterizing a specific type of potential vegetation. Such an increase is observed in the three mains regions of the province of Québec affected by human activities during the last century: Abitibi, Lac Saint-Jean, and Bas-Saint-Laurent (Grondin and Cimon, 2003). The first two of these regions belong to our study area and the third one (temperate zone) has been studied by Boucher et al. (2009). The changes we observed in composition and age structure in Abitibi and Lac-Saint-Jean are mainly the result of two periods of intensive human activities over the course of a century (1910-2010). The first extends from 1910 to 1950 and was characterized by horse logging and log driving (floating logs downriver). Logs were transported to charcoal-powered trains that crossed the southern part of the territory, from the Lac Saint-Jean to Abitibi regions (Figure 3.1). During this period, many human induced fires were started by burning wood embers that fell from trains. We estimate that a significant proportion of the hardwood expansion observed in our study area dates from this period. The second period of intense human activity in the area (1950-2010) was associated with mechanized logging, fuel-powered trains, transport of wood and people by road, and the northward expansion of logging. Since the 1980s, logging techniques have been modified to ensure forest regeneration.

Considering the differences between the modeled natural landscapes and the managed landscape with respect to increase in early successional stages (e.g. *Populus tremuloides* stands) and loss of old forest, we estimated that 5 homogeneous landscapes are outside of their natural range of variability. Similar observations have been reported by many authors (e.g. Foster et al., 1998). These landscapes are considered as resilient because with appropriate silvicultural prescriptions and time, early successional stages vegetation could evolve into late successional stages and closer to the proportion typical of the natural landscape (Holling, 1973; Connell and Sousa, 1983). The changes in forest composition that characterize the 21-pe homogeneous landscape (Abitibi) are considered greater because hardwood expansion (*Populus tremuloides*) favors a steady increase in *Abies balsamea* and a significant decrease in *Picea mariana.* We believe that these changes in forest composition are likely a permanent process. Natural potential vegetation *Picea-Populus* is gradually replaced by managed potential vegetation *Populus-Abies-Picea.* This new managed potential vegetation is considered an alternative state, because the return to a landscape similar to the original one is impossible (Scheffer and Carpenter, 2003; Beisner et al., 2003; Jasinski and Payette, 2005). Some authors have also estimated a change in the natural landscape from the *Picea* domain to the *Abies* domain (Grondin and Cimon, 2003; Laquerre et al., 2009; Arbour and Bergeron, 2011; chapter 2, appendix 6).

Recent loggin is abundant in the majority of homogeneous landscapes (Figure 3.8), and the future forest composition is strongly associated with the development of vegetation after logging (TY2-TY3-TY4). We expected an increase in the proportion of hardwood invasion in *Picea-Populus* (ME1) potential vegetation, which is strongly associated with the Abitibi region, dominated by clay deposits. The process identified in homogeneous landscape 21-pe could be expected to occur in northern regions dominated by mesic clay (221, 231). Large areas have recently been harvested throughout the territory (Ms2, Rs2, Me1), and regeneration is treated by non-commercial thinning with the goal of reducing the proportion of broadleaf species. *Picea*-mosses potential vegetation (Re2) is more subject to invasion by ericaceous species, which is why planting of coniferous species (*Picea mariana, Pinus banksiana*) is prescribed in many stands. The same dynamics characterize *Picea*-sphagnum potential vegetation (Re3), where hydric soils must also be considered a limiting factor when determining silvicultural prescriptions (Harvey et al., 2002; Ministère des ressources naturelles, 2013).

In the context of ecosystem-based management, emphasis should be placed on management strategies that increase both the proportion of old forests (> 100 years) and late-successional species. Modeled natural landscapes should be considered as reference conditions (forest composition) for developping ecosystem-based management strategies, both at the landscape and the local level. Uneven-aged management strategies should be based on the silviculture of both regenerating stands and mature stands. In young stands, the number of broadleaf stems should be reduced. In mature stands, partial cuts should remain the preferred treatment in order to increase the proportion of older stands with an irregular structure (Gauthier et al., 2008). Diversifying silvicultural treatments should be prioritized for maintaining landscape diversity (Harvey et al., 2002) of potential vegetation types and successional stages. The strategies should also consider climate changes that are likely to cause an increase in fires and changes in vegetation. In this context, the target landscape should be characterized by a greater proportion of hardwood that can act as a fire retardant (Boulanger et al., 2013; Terrier et al., 2013), if we really consider that the proportion of early successional stages characterizing the natural landscape is not sufficient.

3.7 Conclusion

This study quantifies the differences between natural and managed landscapes in a large part of the Canadian boreal forest. Gap analysis indicates that the majority of the homogeneous landscape units have been affected by human activities (logging, human-induced fires) and 5 are considered to be outside their range of natural variability. These homogeneous landscapes units are considered resilient, except for the one characterized by a more significant transformation of its forest composition (landscape 21-pe, Abitibi region). Modeled natural homogeneous landscapes are considered as reference conditions in the context of ecosystem-based management. Silvicultural strategies, both at the local and landscape levels, could be developed based on these landscapes. Hardwood expansion, the consequent loss of productive area for coniferous species and loss of forests over 100 years old remain the main issues. Hardwood expansion should be more carefully investigated in order to distinguish more precisely between expansions related to insect outbreaks, colonization and coal steam engines (1870-1940) and recent logging (> 1950). In addition, the reference conditions (natural landscapes) proposed in this study should be linked to the long-term (plurimillennial) variability through paleoecological studies (Reitalu et al., 2014) in order to propose the best reference conditions to the forest practitioners. Knowing the past and the present, the challenge would be to model the natural landscapes on the basis of potential vegetation and successional stages in the future and taking into account climate change.

3.8 Acknowledgements

This study was funded by the Ministère des ressources naturelles du Québec (MRN). Data sources (plots, maps, archives) were collected, managed, and supervised by the staff of the MRN during the 1970-2000 period and we would like to thank each of the individulas involved. Comments by Yan Boucher, Brian Harvey, Paul Jasinski, Jason Laflamme and Germain Mercier, as well as stylistic revisions by Denise Tousignant and Karen Grislis were all greatly appreciated. We would also like to thank Véronique Poirier for her assistance in data analysis and geomatics.

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Figure 3.1 Location of the study area (outlined in red) according to the Ecological Land Classification Hierarchy of the Ministère des ressources naturelles du Québec (Saucier et al. 2009).

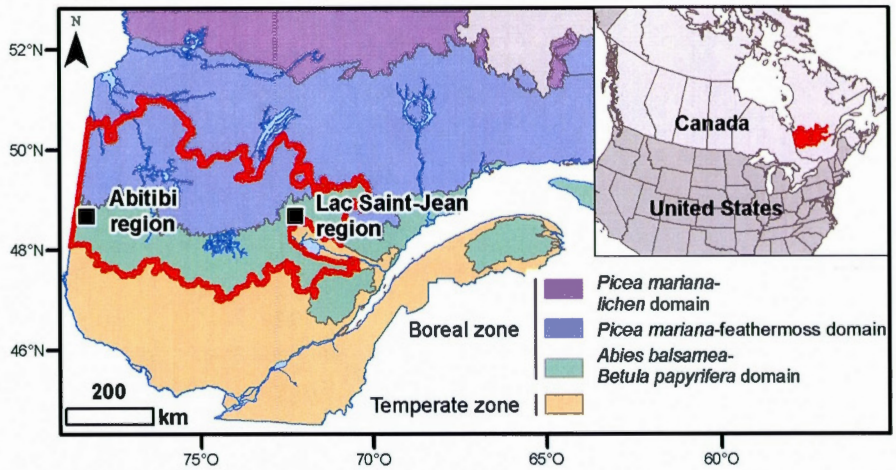
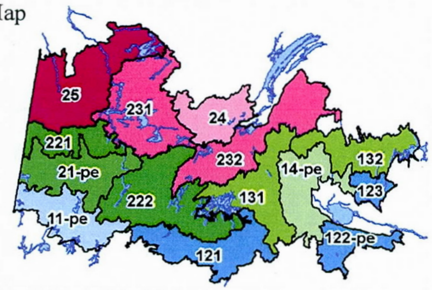


Figure 3.2. Ecological land classification of homogeneous landscape units according to Grondin et al. (2014).

A. Map



B. Description of homogeneous landscapes according to three levels of observation (I, II and III).

Level I	Level II	Level III
Picea mariana-feathermoss domain	Northern portion	**25.** Peatlands and old *Picea mariana* forests
		24. *Picea mariana*, *Pinus banksiana* and peatlands. Young (mineral deposits) and old (organic deposits) forests
		23. *Picea mariana*, Old forests well represented (231-232)
	Southern portion	**22.** *Picea mariana*, *Pinus banksiana*. Young forests relatively abundant (221, 222)
		21-pe. *Picea mariana*, *Populus tremuloides*, *Pinus banksiana*. Strong anthropogenic influence
Abies balsamea-Betula papyrifera domain	Northern portion	**14-pe.** *Picea mariana*, *Populus tremuloides*, *Pinus banksiana*, *Betula papyrifera*. Strong anthropogenic influence
		13. *Picea mariana*, *Betula papyrifera*, *Abies balsamea*. Young (131, *Pinus banksiana*) and old (132) forests well represented
	Southern portion	**12.** *Betula papyrifera*, *Picea mariana*. Forests affected by insect outbreaks and fires (121, 122-pe, 123)
		11-pe. *Betula papyrifera*, *Picea mariana*, *Populus tremuloides*. Strong anthropogenic influence

Table 3.1. Description of homogeneous landscape units according to some explanatory variables.

Homogeneous landscape	Area (%)	Climate		Physical environment			Natural disturbances					Human disturbances		
		Gdd	Preci	Ele	D_4ga	D_7	Sbom	1921	1891	1851	1951	Log1	Hf1	1951h
25	12	1111	287	11	7	59	0	15	14	71	3	0	0	0
24	5	1139	316	26	3	23	0	34	17	49	9	1	2	0
232	10	1149	330	38	0	9	1	21	24	56	4	1	1	0
231	11	1165	312	25	40	13	3	31	20	50	3	1	1	0
222	11	1274	334	39	4	12	4	41	25	35	13	7	4	0
221	4	1201	312	23	58	16	2	47	14	39	0	8	3	5
21-pe	7	1258	312	24	44	18	3	39	9	52	0	13	15	14
14-pe	7	1281	316	64	0	1	3	34	21	45	0	15	7	28
132	6	1195	346	73	0	2	12	27	33	41	0	10	3	4
131	8	1210	328	56	0	4	3	35	31	33	0	14	2	10
123	2	1276	359	90	0	1	34	40	25	35	0	22	5	9
122-pe	3	1340	345	70	0	2	14	52	11	37	0	13	18	7
121	7	1295	342	77	0	1	26	40	23	37	0	16	2	11
11-pe	6	1345	303	27	34	17	11	35	14	51	0	10	32	16

Gdd : Annual number of growing degree-days (bios)

Preci : Rainfall during the growing season (mm) (bios)

Ele : Absolute difference between the highest and lowest elevation of an ecological district (topographic elevation) (m) (ded). Ele > 40 : hilly topography, ele 20-40 : undulated topography, ele < 20 : flat topography

D_4GA : Area (%) covered by glaciolacustrine fine-textured (clay) surficial deposit (ded)

D_7 : Area (%) covered by organic deposits (ded)

Sbom : Area (%) covered by light spruce budworm outbreaks (gs2)

1921 period : Relative proportion of plots originating from 1901 to 1930 (fip)

1891 period : Relative proportion of plots originating from 1870 to 1900 (fip)

1851 period : Relative proportion of plots originating before 1870 (fip) (see appendix A.3)

1951 period : Relative proportion of plots originating from natural disturbances after 1930

Logl : Relative area covered by logging during the 1970 period (gs1)

Hfl : Frequency of human-induced fires per 100 km^2 during the period 1938-1998 (anhd)

1951h : Relative proportion of plots originating from human disturbances after 1930

Data sources: anhd : archival data of natural and human disturbances, bios: BioSIM software, ded: database of ecological districts, fip: forest inventory plots, gs1: geospatial database Sifort-1 (forest maps 1970-1980), gs2: geospatial database Sifort-2 (forest maps 1980-1990).

Figure 3.3. Method used to model the natural landscape according to fire cycle, age structure and forest composition (A), to define the managed landscape (B) and to compare both landscapes (C)

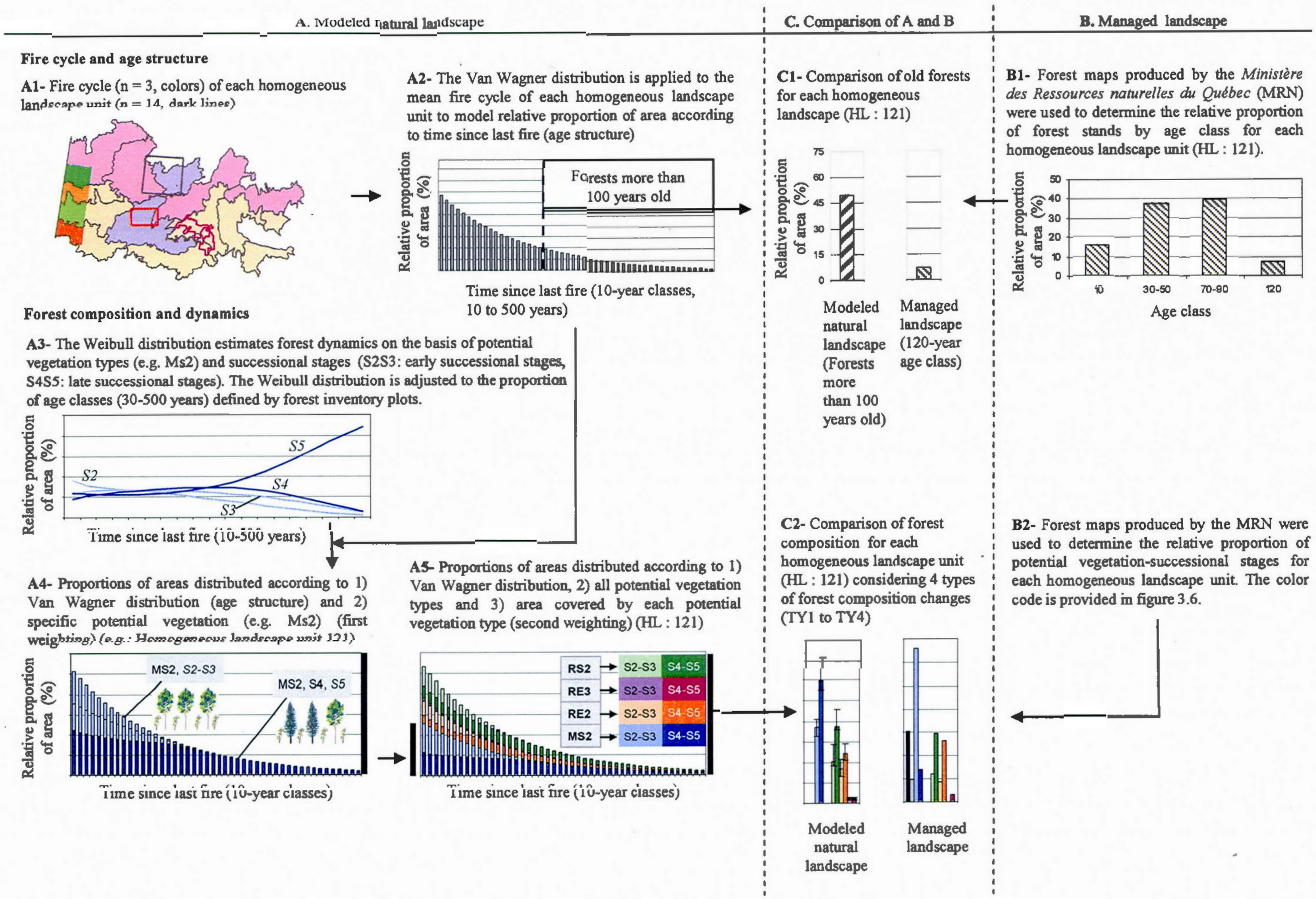


Figure 3.4. Contemporary fire cycles (C1-110 years; C2-140 years and C3-180 years) characterizing the study area. Homogeneous landscapes units are delineated by dark lines. Fire origin maps (F1 to F8) used to define a fire cycles are shown. F1 to F4 (colors) correspond to the Abitibi region of Bergeron et al. (2001), F5 (Cyr et al. 2005), F6 (Bergeron et al. 2001), F7 (Le Goff et al. 2007) and F8 (Lesieur et al. 2002).

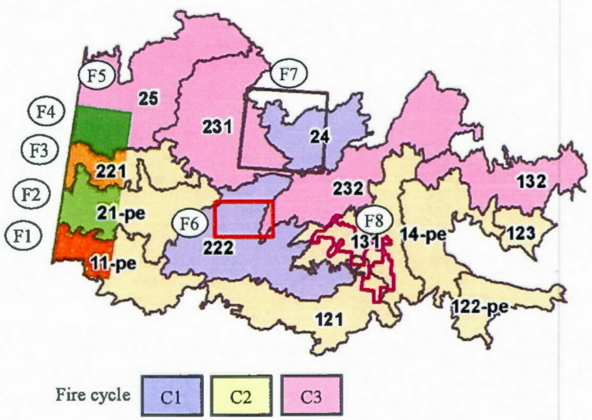
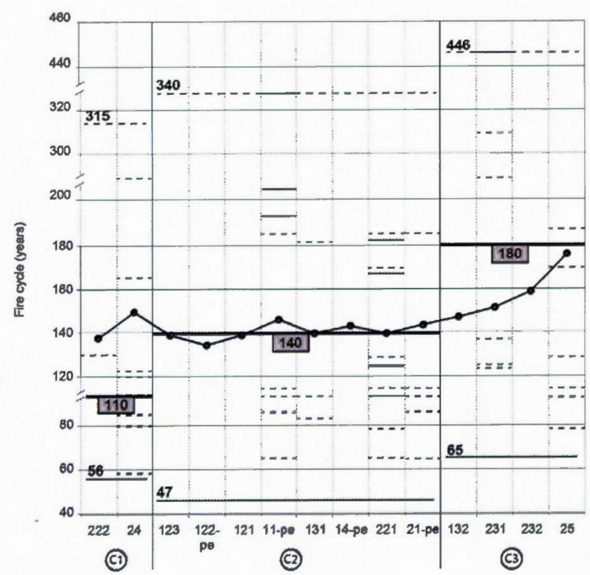


Figure 3.5. Temporal variability of the 14 homogeneous landscapes units with regard to their fire cycles variability. C1 (110 years), C2 (140 years) and C3 (180 years) are the contemporary fire cycles.



Fire cycle estimated by the forest inventory plots

Mean fire cycle used to define the natural landscape

Longest fire cycle used to estimate the variability of the natural landscape

Shortest fire cycle used to estimate the variability of the natural landscape

Contemporary fire cycles (1750-1920) defined in the literature (Figure 3.4,

Holocene fire cycles defined in the literature (Appendix A1). The values 340 and 446 are also related to Holocene.

Figure 3.6. Forest composition and forest dynamics defined by 5 potential vegetation types (e.g. Ms2) and 4 successional stages (S2, S3, S4, S5). Code definitions are provided in figure 3.8 and appendix B1.

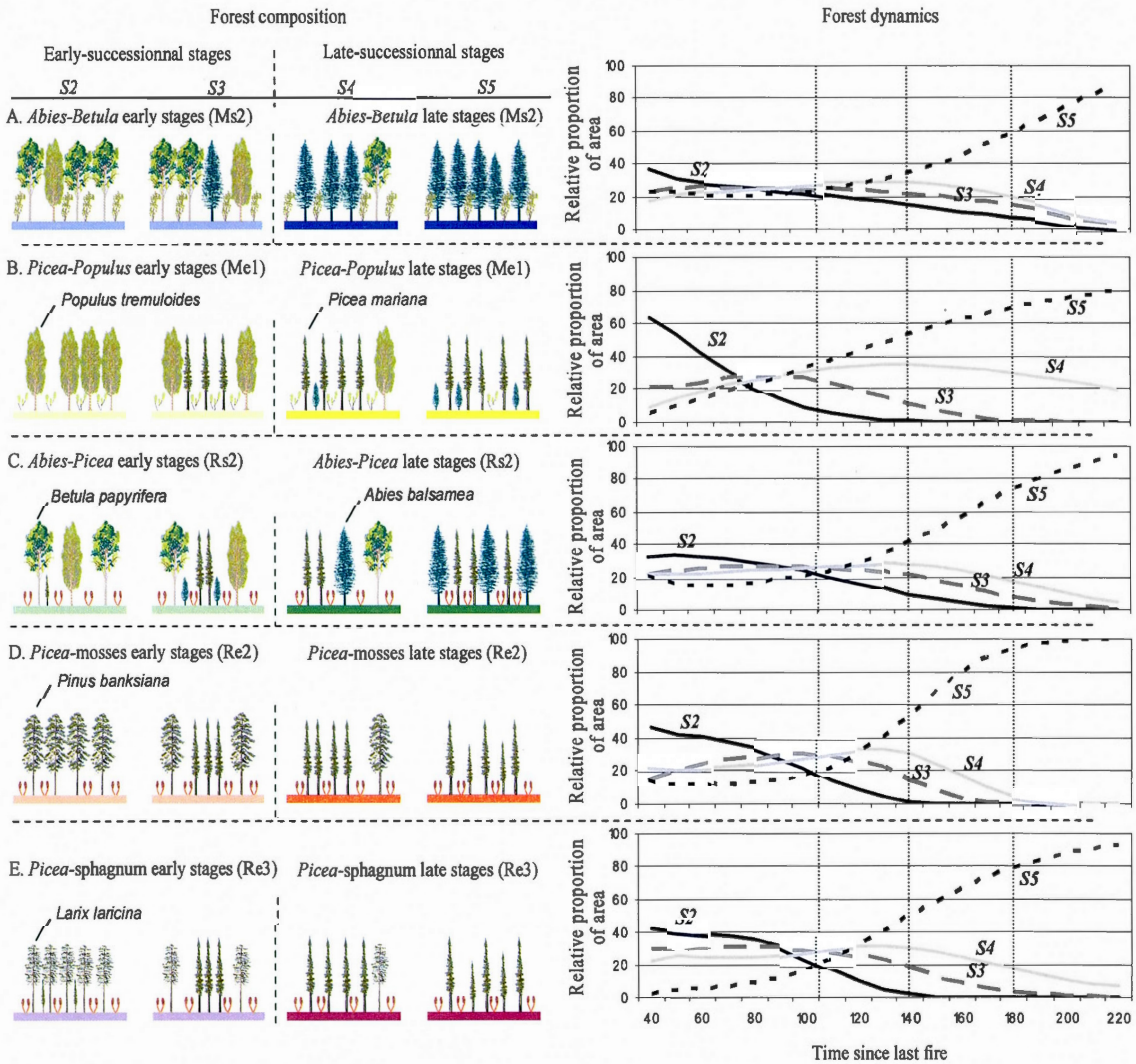


Figure 3.7. **A**. Ordination diagram showing the magnitude of changes in forest composition from natural to managed landscapes. Each vector of the ordination diagram represents one homogeneous landscape unit. Homogeneous landscape units are grouped according to four geographically distinct changes of forest composition types (TY1 to TY4). **B**. Map showing the spatial distribution of the four types of changes. Code definitions are provided in figure 3.8.

A. Ordination diagram and the four types of forest composition changes

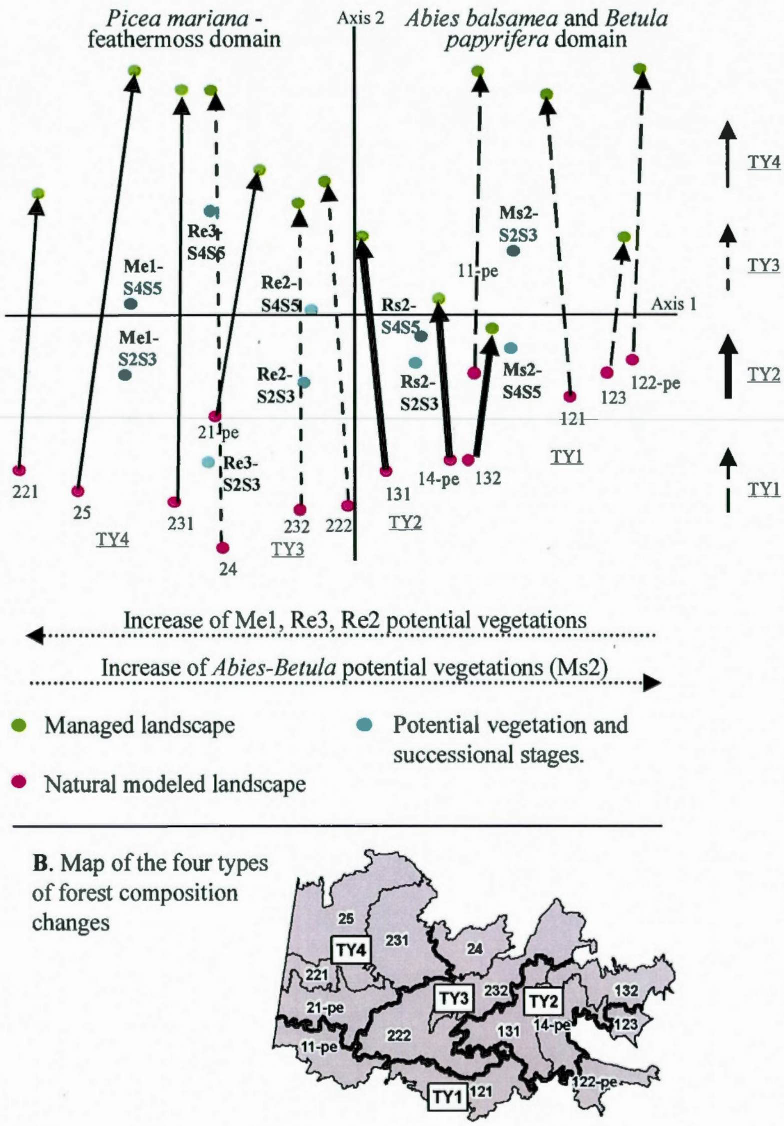


Figure 3.8. Comparison of four homogeneous landscape units (e.g. HL: 121) representing the four geographically distinct forest composition (TY1 to TY4) with respect to their natural and managed forest composition. The modeled natural landscape is defined using fire cycle variability (Figure 3.5) and forest dynamics (Figure 3.6). Managed landscape composition is characterized from forest maps (1990-2000, the MRN's third 10-year inventory program). Colors represent forest composition related to potential vegetation types and successional stages.

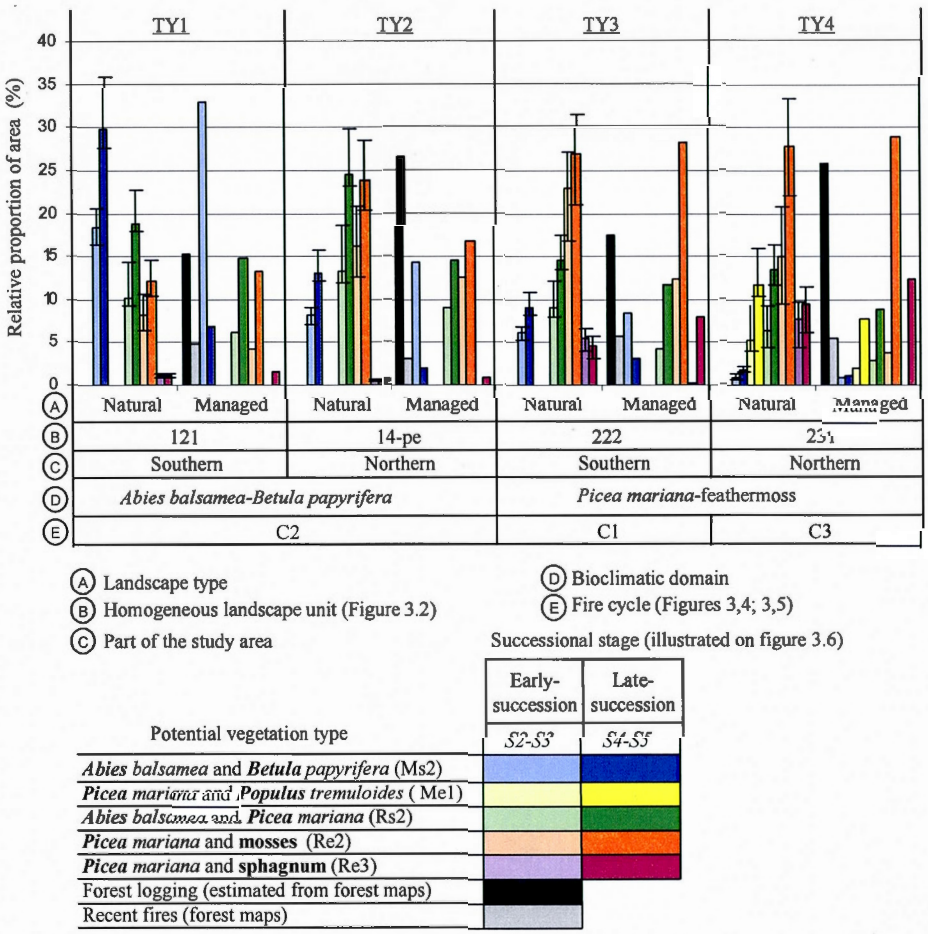


Figure 3.9. A1-A2 : Comparison of four homogeneous landscape units (e.g. HL: 121) representing the four geographically distinct changes of forest composition (TY1 to TY4) with respect to their natural and managed forest composition and B: expansion of this comparison for the 14 homogeneous landscapes in the goal to identify those that are outside of their natural variability. C-D-E : relation between logging, hardwood expansion and homogeneous landscape units outside of their natural variability

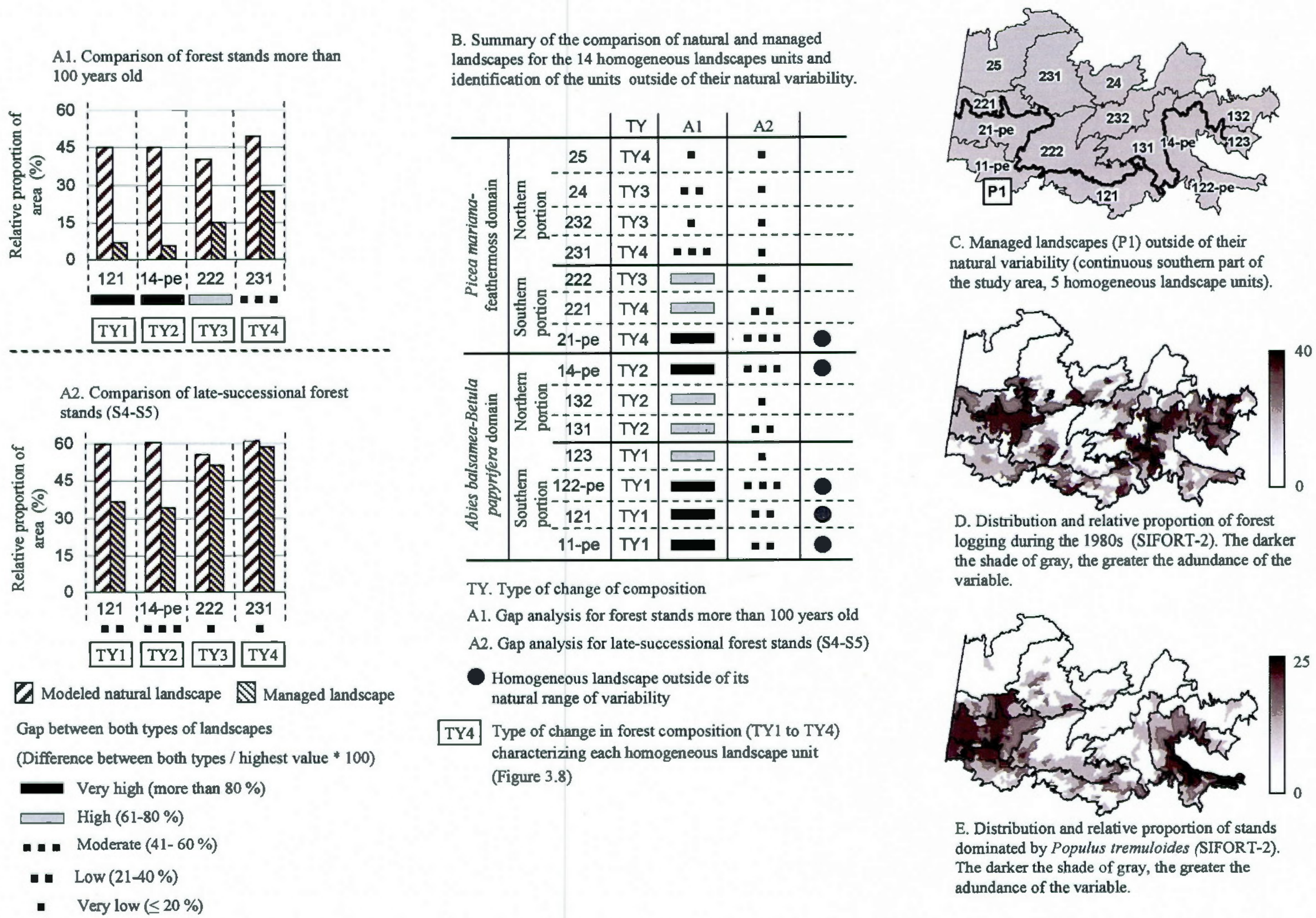


Figure 3.10. Comparison of the five homogeneous landscape units (e.g. HL: 121) considered outside of their natural range of variability in relation to their natural and managed landscape. Potential vegetation and successional stages are represented by colors : *Abies-Betula* early successional stages (Ms2-S2S3, light blue color) and late successional stages (Ms2-S4S5, dark blue color), *Picea-Populus* early successional stages (Me1-S2S3) and late successional stages (Me1-S4S5) (Figure 3.8).

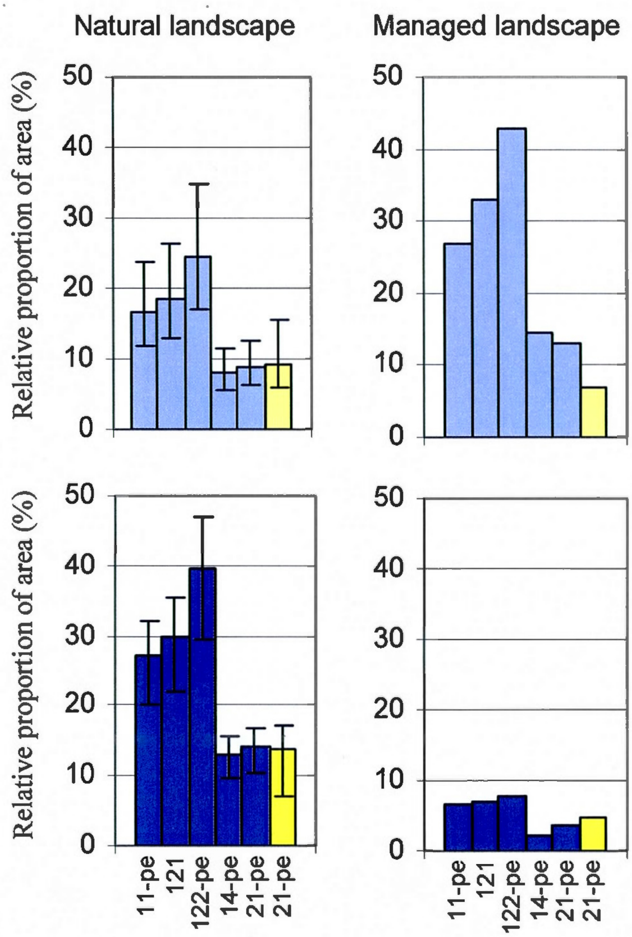
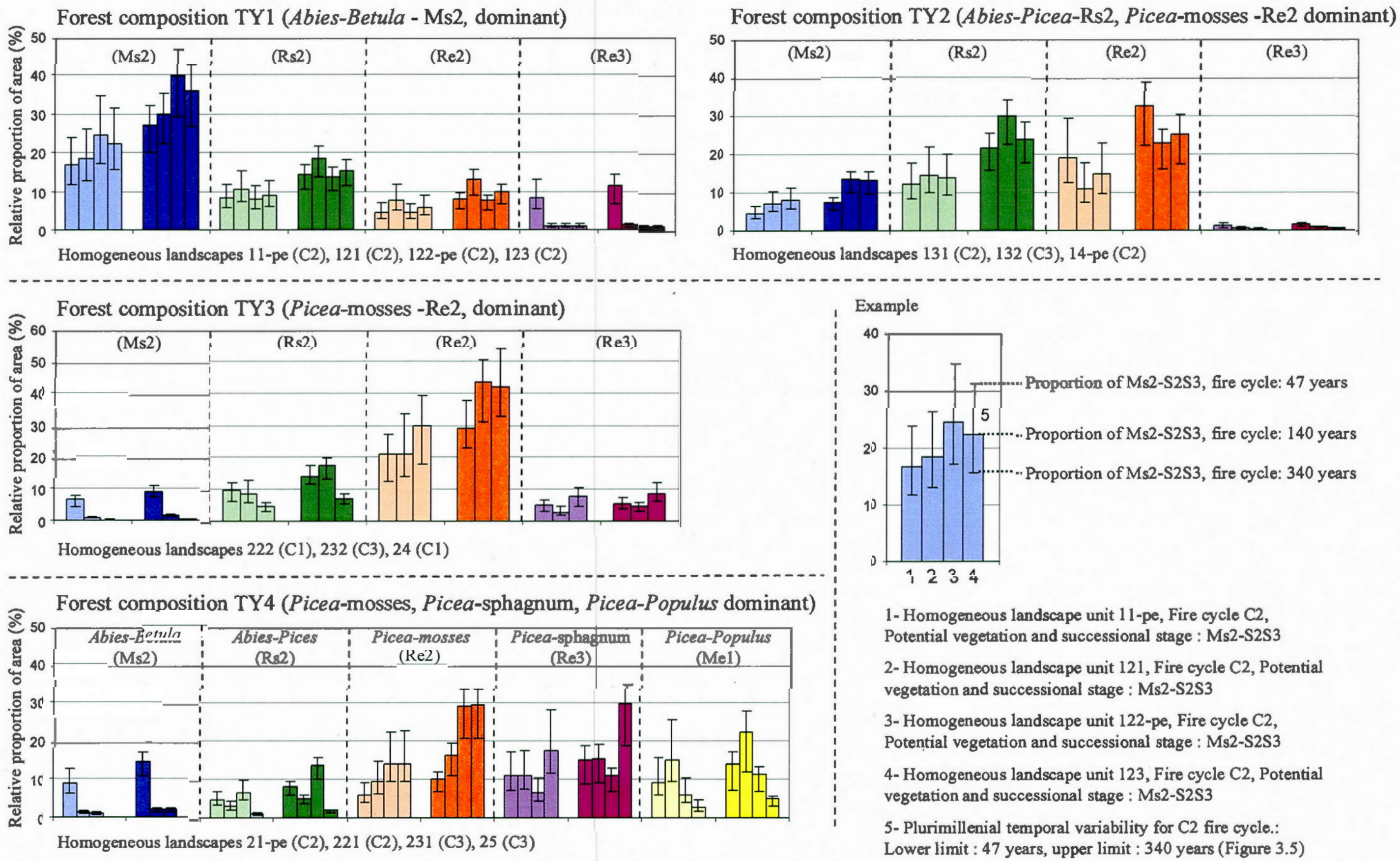


Figure 3.11: Modeled natural landscapes of the 14 homogeneous landscapes units characterizing the study area (Figure 3.2). The landscapes are described according to four types of forest composition (TY1-TY4, Figures 3.7, 3.8) and combinations of potential vegetation-successional stages represented by colors (Figure 3.8). Each combination is defined by a temporal natural variability estimated on the basis of three fire cycles (C1, C2, C3) (Figures 3.4, 3.5)



3.10 Appendices

Appendix A. Determining the fire cycle and an age structure for each homogeneous landscape unit

Appendix B. Determining the forest composition for each homogeneous landscape unit

Appendix C. Comparing natural and managed landscapes for each homogeneous landscape unit

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APPENDIX A.

DETERMINING THE AGE STRUCTURE FOR EACH HOMOGENEOUS LANDSCAPE UNIT

In order to model the natural landscape (Figure 3.3), it is necessary to assign a fire cycle (Figure 3.3A1) and an age structure (Figure 3.3A2) to each homogeneous landscape unit. A summary of the method used is presented in the main text of this study. A more detailed description is provided in this appendix.

1- Contemporary fire cycle and age structure defined in the western portion of the study area

The first step in determining the fire cycles was to analyze of information presented in the literature, particularly the fire origin maps produced by Bergeron et al. (2001) and Le Goff (2007). The area analyzed by Bergeron et al. (2001) (Figure 3.4, sectors F1 to F4, Appendices A1, A2c) corresponds to a portion of the four homogeneous landscape units we studied: 11-pe, 21-pe, 221, and 25. The fire origin map (F1 to F4) is characterized by a dominance of fires that occurred around 1920 and 1916 (Appendix A2a). A synthesis of the detailed age class distribution (ten years) into longer periods reveals a dominance of fires in the 1851 period (prior to 1870) and a sub-dominance in the period 1921 (1901-1930) (Appendix A2a). This age structure indicates that the proportion of forest stands more than 100 years old (1851 and 1891 periods) is close to 60%. This description of the fire periods corresponds to a fire cycle of approximately 140 years (Bergeron et al., 2001). The area analyzed by Le Goff (2007) (sector F7, Figure 3.4 and Appendix A2c) corresponds mainly to a portion of homogeneous landscape unit 24. The fire origin map is characterized by a dominance of fires that occurred in 1920 and 1980 (Appendix A2b). This age structure indicates that the proportion of forest stands more than 100 years old (1851 and 1891 periods) is close to 30%. According to Le Goff et al. (2007), this age structure corresponds to a fire cycle of approximately 100 years for the immediate post-Little Ice Age period (Appendix A1). The variation around this mean value is relatively high (80-122).

2- Comparison between the age structure defined in the western portion of the study area and forest inventory plots (MRN).

With the goal of defining a fire cycle for each homogeneous landscape unit, we extrapolated the available knowledge (fire origin maps for 8 landscapes) to the total number of homogeneous landscape units (n=14). To extrapolate the fire cycles, we mainly used the forest inventory plots produced by the Ministère des ressources naturelles (MRN) (Appendices A3, A4, A5). To evaluate the quality of forest plots necessary to adequately define a fire cycle, we compared the distribution of fire periods for portions F1 to F4 described first, by the forest origin map elaborated by Bergeron et al. (2001), and second, by the forest inventory plots of the MRN (Appendix A6). Initially, we encountered a problem with forest plots originating from human disturbances (human fires, logging). These plots mainly correspond to the

1951 period (after 1930) and exhibit a high relative proportion of the total number of plots produced in homogeneous landscape units heavily affected by human activities (Appendix A4). Considering the strong resemblance between the areas affected by human activities (Appendix A5a) and plots of the 1951 period (Appendix A5b), we hypothesized that the plots that are both 1) classified in this recent period (1951) and 2) located in the logging area (southern part of the study area) originated from logging conducted in old forests (1851 period). We therefore grouped the stands of the 1951 period with those of the 1851 period for the portion of the study area affected by human activities (Appendix A5f). The impacts of human activities are numerous in the southern part of the territory, as indicated by the rarity of forest stands from the 1851 period (Appendices A5c and A5d) and the mean age of forests, less than 75 years (Appendix A5e). Appendix A5f shows the relative proportion of stands originating from the "natural 1851 period" with the goal of calculating a "natural fire cycle".

3- Determination of fire cycles

3.1 The relative proportion of forest inventory plots belonging to each period of origin

The MRN forest inventory plots have been used to extrapolate a fire cycle for each homogeneous landscape unit (n=14) (Appendices A8, A9) from the fire origin maps produced by various authors (Appendix A1). The relative proportion of forest inventory plots belonging to different periods of origin (1851, 1891, 1921, 1951) was used to calculate a mean age origin (fire cycle) for each homogeneous landscape unit. Considering the large number of plots (Appendix A3), the proportion of plots of various ages can be considered as a proportion of area. The method used to define the fire cycle (relative proportion of plots by period) is consistent with those used by

Bergeron et al. (2001) and Payette (2010). These fire cycles are considered as the average age of forests stands developed after the last contemporary fire.

We have improved the classification of homogeneous units by placing them into a specific fire cycle by analyzing 1) the distribution and abundance of *Pinus banksiana*, a species strongly associated with fire, 2) the distribution and abundance of *Abies balsamea*, a species associated to late-successional forests and 3) the relationship between 1851 fire origin period and the relative abundance of organic deposits (Appendix A7). *Pinus banksiana* is relatively abundant (15%) in the homogeneous landscapes well provided by sandy deposits. *Abies balsamea* favours the eastern part of the study area (landscapes 222 and 24). Organic deposits are more abundant in the *Picea mariana*-feathermoss domain than in the *Abies balsamea-Betula* papyrifera domain.

Appendix A8 shows that most of the homogeneous landscape units have a fire cycle close to 140 years. This result is similar to Bergeron et al. (2001), and is considered as the basis of our second fire cycle (C2, Appendix A1). More specifically:

- Four homogeneous landscape units belonging to the second fire cycle (C2) are slightly dominated by stands of the 1921 period. Stands from the 1851 period are well represented (123, 122-pe, 121, 221) (Appendix A9). This representation is similar to that provided by Bergeron et al. (2001) for the F3 landscape portions (Appendix A6). The fire cycle of these landscapes is slightly less than 140 years (Appendix A8).

- Three landscapes also belonging to the second fire cycle (C2) are dominated by stands of the 1851 period (11-pe, 14-pe and 21-pe). This representation is similar to that calculated by Bergeron et al. (2001) for sectors F1 and F2 (Appendix A6). The fire cycle of these landscapes is slightly longer than 140 years (Appendix A8).

- Landscapes 131 and 132 are quite similar relative to the proportion of the three periods of fire origin (Appendix A9). Landscape 131, characterized by a fire cycle of 123 years for the 1850-1920 period (Appendix A1, sector F8), is classified within the second fire cycle on the basis of Lesieur et al. (2002). In this homogeneous landscape unit (131), the relative proportion of *Pinus banksiana* is similar to that in other homogeneous landscape units classified with the second fire cycle (14-pe, 21-pe, 221) (Appendix A7a). Landscape 132 is classified within the third fire cycle on the basis of a relatively low proportion of *Pinus banksiana* (Appendix A7a) and the highest proportion of *Abies balsamea* (AbbaF, Pima_AbbaF) of all the homogeneous landscape units (Appendix A7b). Landscape 132 is also close to the area studied by Bélisle et al. (2011), characterized by a fire cycle of 247 years and classified as part of the eastern part of the *Picea mariana*-feathermoss domain (Saucier et al., 2009).

- Landscapes 222 and 24 are different relative to the proportion of fire periods origins (Appendix A9). The 1851 period is dominant in landscape 24 and sub-dominant in 222. These two landscapes are considered as a specific fire cycle (C1) based on data collected by Legoff et al. (2007) and Bergeron et al. (2001). These two authors presented some fire cycles less than or close to 110 years (Appendix A1). These two landscapes are characterized by the highest proportions of sandy deposits and *Pinus banksiana* (Appendix A7a) and a low abundance of *Abies balsamea* (Appendix A7b). Landscape 24 is unique due to its relatively high abundance of organic deposits and stands originating from the 1851 period (Appendix A7c). Units 222 and 24 are described by considering two fires cycles, the first for their mineral soil (short fire cycle) and the second for their organic deposits (long fire cycle). In the context of the present study, the classification of homogeneous landscape unit 24 with C1 is justified by data from Le Goff et al. (2007), who showed a dominance of the 1921 and 1951 periods (Appendix A2b).

- The homogeneous landscape units associated with the C3 fire cycle are characterized by a relatively high proportion of stands of the 1851 period (231, 232, 25) (Appendix A9). The difference between the plots of the 1851 period and those of the 1921 period is approximately 15-20%. This difference reaches more than 50% for landscape 25. The high proportion of stands of the 1851 period suggests the presence of a specific fire cycle in unit 25. However, considering the results presented by various authors (Appendix A1), which are close to 170-180 years, and also in the idea to limit the number of fire cycles, we preferred to classify landscapes 231, 232 and 25 in this last fire cycle (Figure 3.4 and Appendix A9).

3.2 Proportion of forests more than 100 years old and spatial variability of the homogeneous landscapes units

The description of the study area according to the proportion of forest more than 100 years old (Appendix A10) is considered complementary to the previous classification of each homogeneous landscape unit with regard to a fire cycle (Appendices A1, A7, A8, A9). The objectives of this section are to define a spatial variability for the three fire cycles and to compare it to the temporal variability (Figure 3.5, Appendix A1). We conclude that the temporal variation, which consider three periods : 8000 to 500 years BP, 1550-1850 (calendar years), and 1850-1920 (calendar years), is greater than the spatial variability. In the main portion of the article the spatial variability was mainly addressed concerning three fire cycles. We show in this appendix that this variability could have been more detailed in the sense that it would have been possible to define a spatial variability around each of the three fire cycles.

The description of the forests more than 100 years old is based on three sources of information: forest inventory plots (MRN), geobase SIFORT-1 (description of forest maps produced in the 1970s) and geobase SIFORT-2 (forest maps produced in the 1980s). The first source considers the proportion of forest plots belonging to the 1851 period (sum of 1951 and 1851 periods for the landscapes heavily affected by human activities). The second source refers to the proportion of mature forests delineated on maps produced in the 1970 period (*SIFORT*-1). The third source corresponds to the 90- and 120-year old forests characterizing the maps of the 1980 period (*SIFORT*-2). Considering the importance of logging in the southern part of the territory, the third source of information is composed of the sum of the area covered by forest stands 90 and 120 years old added to area that has been affected by recent logging. We assume that the logging activities must have been conducted in old stands and must therefore be considered in the evaluation of forests more than 100 years old. In addition to the information from these three sources, we included the fire cycle presented in our analyses related to this topic (Appendix A8) and the proportion of forests determined in the baseline studies (Appendix A1).

- The description of forests more than 100 years old shows important differences between landscapes belonging to the second (C2) and third (C3) fire cycles. For example, the proportion of forest stands 90 and 120 years old, added to forest logging (SIFORT-2), is clearly more important in landscapes 132, 231, 232, and 25 than in the other landscapes, and these landscapes are classified with the third fire cycle (C3). In this last fire cycle (C3), homogeneous landscape unit 25 is still distinguishable from those of the same fire cycle. The proportion of old forest is always greater than 60% and often reaches 70%, which is similar to the Abitibi Model Forest located in Ontario in a landscape dominated by peatlands (Bergeron et al., 2001). The variables used to construct Appendix A10 do not allow us to distinguish homogeneous landscape units 222 and 24, classified with the first fire cycle. The justifications for considering these two landscapes as a specific fire cycle (C1) were provided previously (section 3.1).

- Appendix A10 has also been used to compare the proportion of forests more than 100 years old with the proportion of old forest deduced from the fire cycle presented in our baseline studies (Table 3.2, Appendix A1). In the majority of the landscapes, the proportion presented in the baseline studies is located in the upper portion of the spatial variability.

- Finally, appendix A10 allows us to define the spatial variability of the three fire cycles considered in this study. This variability is less important than temporal variability. For example, the second fire cycle has an estimated spatial variability ranging from 80 to 150 years and a temporal variability ranging from 47 to 340 years (Appendix A1).

4- Description of the fire cycles in relation to forest composition

The goal of this section is to give more informations on the links between 1) fire cycle spatial distribution and 2) vegetation on mesic soils. These links have been briefly presented in the main part of this study and in the discussion.

Appendix A11 clearly shows the geographical changes in forest composition from the southern part of the *Abies balsamea – Betula papyrifera* domain to the northern part of the *Picea mariana*-feathermoss domain. In the southern part of the *Abies balsamea – Betula papyrifera* domain, *Abies-Betula* (Ms2) potential vegetation type dominates the landscapes. In the northern part, *Abies-Betula* (Ms2) is still present, but *Abies-Picea* (Rs2) and *Picea*-mosses (Re2) potential vegetation types are dominant. In the southern part of the *Picea mariana-feathermoss*, homogeneous landscape 222 is dominated by *Picea*-mosses (Re2) and *Abies-Betula* (Ms2) potential vegetation types. The two others homogeneous landscape units of this portion of the southern domain are formed mainly by early successional stages (S2S3) of various potential vegetation types. Finally, the northern part of the *Pices mariana*- feathermoss domain is dominated by *Picea*-mosses potential vegetation (Re2). *Pinus banksiana* is abundant in landscape 24.

The shortest fire cycle (C1- 110 years) was observed in two landscapes (222, 24) where *Pinus banksiana* on mesic till is abundant (more than 15%). The intermediate fire cycle (C2- 140 years) characterizes numerous homogeneous landscapes belonging to the southern part of the *Picea mariana*-feathermoss domain and to the *Abies balsamea-Betula papyrifera* domain (MacLean and Bedell, 1955; Cogbill, 1985; Bergeron et al., 2001, 2004; Lesieur et al., 2002).

To explain this homogeneity in the second fire cycle (C2) on such distinct landscapes, Bergeron et al. (2004) hypothesizes that the various areas are not distinguished by their fire cycle, but by fire severity. Gauthier et al. (2000) indicated that changes in vegetation and fire severity are strongly associated with topography: hilly topography would be favorable to fires of low severity, topographic refuges (sheltered sites) and *Abies balsamea* development. Mansuy et al. (2010) demonstrated that in areas with a relatively short fire cycle, distinct physical environments may have the same fire cycle.

The longest fire cycle (C3- 180 years) was observed in conditions opposite to the first. Based on vegetation and the physical environment characteristics, we also observed two different sectors.

- The first sector (central and eastern area, 231, 232, 132) is dominated by *Picea*-mosses potential vegetation (Re2) (231 and 232) or by *Abies-Picea* potential vegetation (Rs2) (132) (Appendix A11), where organic deposits cover less than 15% of the area (Table 3.1);

- A second sector, characterizing the northwestern end (landscape 25), consists mainly of *Picea*-sphagnum potential vegetation (Re3), and organic deposits abound. On mesic soils, *Picea-mosses* potential vegetation dominates and *Pinus banksiana* (Re2-S2S3) is rare. Charred wood fragments (^{14}C) in peat or in contact with organic and mineral soils dates fires from 350 to 2500 years (Cyr et al., 2005; Simard et al., 2007). Cyr et al. (2005) proposed a fire cycle of 446 years for the period prior to 1850 (Appendix A1). This information is included in the variability we ascribed to our third fire cycle (65-446 years).

We conclude than even if this study aims to understand the landscape heterogeneity in regard to various ecological process, some aspects of natural disturbances and their relationships to vegetation are not well understand.

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5- Age structure

Once the fires cycles (Appendices A1 to A10) and their variability in regards to vegetation (Appendix A11) are known, the next step is to define the age structure of each homogeneous landscape unit (Figure 3.3A2). The age structures were defined by considering a sequence of mathematical equations. Each of 14 homogeneous landscape units considered in this study (Figure 3.2; Grondin et al., 2014) was coded as u_k and belongs to the set U (Appendices A12 and A13, eq. A1). We defined a set of parameters $\{C_1, C_2, C_3\}$ for the three fire cycles introduced in the previous steps. From these three fire cycles, the set U was partitioned so that two homogeneous landscape units were classified within the first fire cycle (110 years), eight within the second (140 years), and four within the third (180 years). Using this information, we defined the age structure by using the Van Wagner distribution (Van Wagner, 1978; Johnson and Van Wagner, 1985).

The original model of Van Wagner considers the frequency of an age class t as being the probability of reaching age t before the next fire. This formula is equivalent to recognizing a distribution function underlying the fire phenomenon. This distribution is also known as a Bernoulli function and assumes that a fire with a constant annual probability p occurs after t years. This fire was preceded by a number t of successive years without fire $(1\text{-}p)^t$ which gives the distribution $p\ (1\text{-}p)^t$. When the probability p is a low value (e.g 0.05 in the case of one fire per 20 years), it is demonstrated that $(1\text{-}p)^t$ can be approximated well by $exp(-p)$ and give $p\ exp(-pt)$ in replacement of $p\ (1\text{-}p)^t$. This last equation is also known as the p-parameter negative exponential distribution with the parameter $p=1/c_k$ where the c_k parameter describes the fire cycle defined above.

The proportion of area H of each homogeneous landscape unit for which the fire cycle c_k is known can be calculated. In this study, t correspond to age classes of 10 years codified I_j (Appendices A12 and A13, eq. A2). The lower limit of the age class is included in the class and the upper limit excluded. For example, in the age class [10, 20), 10 corresponds to the maximum value associated to [0, 10) and 20 does not belong to the class [10, 20). Each value of H corresponds to the relative proportion of area occupied between a specific ten years age class I_j since the beginning (10 years) and the end of the distribution which may correspond to 500 years or more. We are interested in evaluating the relative proportion of area in percent (e_j) attributed to each ten years age class I_j. Sufficient proportions of areas for age classes located beyond 500 years may remain, so that the sum of the relative proportions of areas e_j may be less than 100%. These residual areas are distributed proportionally to the area by age class I_j (Appendices A12 and A13, eq. A3). The proportions of areas not considered in the interval 10-500 years increase with the fire cycle. For example, in a fire cycle of 300 years, nearly 20% of the area exceeds 500 years.

The proportion of forests more than 100 years old, denoted f100, is calculated by summing the relative proportion of areas (e_j) with age classes greater than or equal to 100 years. $G(c_k)$ is the proportion of forests more than 100 years old with a specific fire cycle c_k. This proportion can be evaluated directly (Appendices A12 and A13, eq. A4). At the opposite, when the proportion of forests more than 100 years old is known, it is possible to directly define the value of *f100* (fire cycle) of a homogeneous landscape unit (Appendices A12 and A13, eq. A5). From this cycle, the model of Van Wagner allows the age structure of each homogeneous landscape unit to be built (Appendices A12 and A13, eq. A2, A3, A4).

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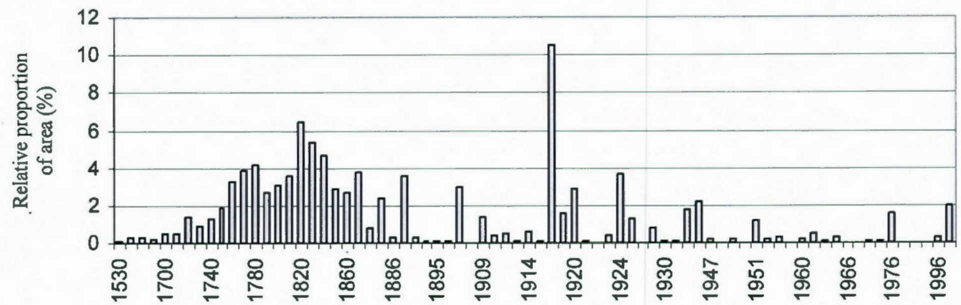
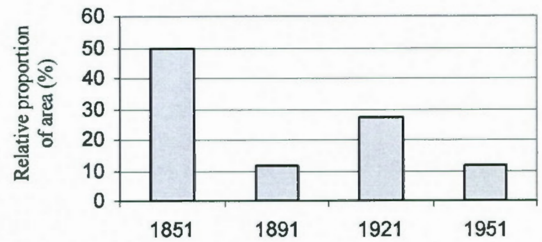
Appendix A1. Fire cycles considered in this study (C1 to C3) are based on fire origin maps (F1 to F8). Fire cycles were computed for the following predetermined periods: Holocene before the Little Ice Age (8 000-500 years BP), Little Ice Age (1550-1850) and 1850–1920. The 1550 and 1850 limits between periods were selected because they corresponds to the Little Ice Age, while 1920 corresponds to the beginning of the intensive colonization of the region.

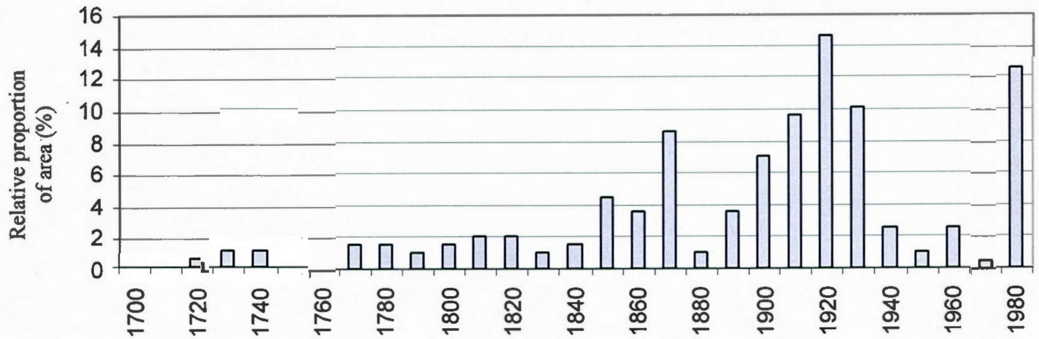
Fire cycle (Fire cycle variability)	Homogeneous landscape	Reference studies				
		Fire cycle (years) (spatial variability)	Cycle by period (years)			Author and location in the study area (Figure 3.4)
			Temporal holocene variability	Temporal contemporary variability		
				1550-1850	1850-1920	
C1- 110 years (56-315)	222	111			86 (56 à 131)	Bergeron et al. 2001, Abitibi east - **F6**
	24	130 (102-166)				Le Goff et al. 2007, NE and SE - **F7**
		85 (59-122)				Le Goff et al. 2007, NE - **F7**
		166 (120-230)				Le Goff et al. 2007, SE - **F7**
				164 (85-315)	99 (80-122)	Le Goff et al. 2007, global results by period
C2- 140 years (47-340)	11-pe	139		83 (65-105)	146 (114-187)	Bergeron et al. 2001, Abitibi west - **F1-F2-F3-F4**
		145				F1 area of Bergeron et al. (2001) estimated in the present study
				83 (65-105)	111 (88-140)	Bergeron et al. 2004, mixedwood region - **F1, F2**
			230,340,192			Carcaillet et al. 2010
	221	139		83 (65-105)	146 (114-187)	Bergeron et al. 2001, Abitibi west - **F1-F2-F3-F4**
		139				F3 area of Bergeron et al. (2001) estimated in the present study
				101 (79-129)	135 (108-171)	Bergeron et al. 2004, coniferous region - **F3, F4**
			96,166,125,182			Carcaillet et al. 2010
	21-pe	139		83 (65-105)	146 (114-187)	Bergeron et al. 2001, Abitibi west - **F1-F2-F3-F4**
		143				F2 area of Bergeron et al. (2001) estimated in the present study
				83 (65-105)	111 (88-140)	Bergeron et al. 2004, mixedwood region - **F1, F2**
	131	127		69 (47-102)	123 (83-181)	Bergeron et al. 2001, central Quebec, Lesieur et al. 2002 - **F8**
C3- 180 years (65-446)	231	188 (126-310)				Le Goff et al. 2007, NW - **F7**
		170 (124-234)				Le Goff et al. 2007, SW - **F7**
		178 (138-232)				Le Goff et al. 2007, NW and SW - **F7**
	25	139		83 (65-105)	146 (114-187)	Bergeron et al. 2001, Abitibi west - **F1-F2-F3-F4**
		174				F4 area of Bergeron et al. (2001) estimated in the present study
				101 (79-129)	135(108-171)	Bergeron et al. 2004, coniferous region - **F3, F4**
			446			Cyr et al. 2005 - **F5**

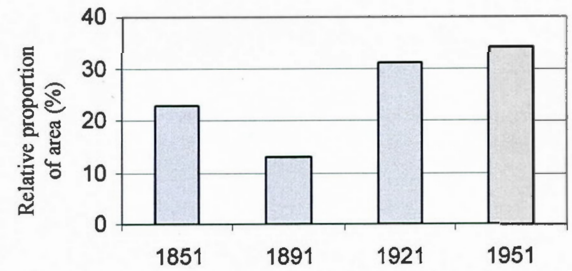
Appendix A2a. Area and year of origin of contemporary fires in the western end of the study area defined by Bergeron et al. (2001) (Figure 3.4, F1 to F4). Years of origin are synthesized using 4 classes: 1851 (prior to 1870), 1891 (1870 to 1900), 1921 (1901 to 1930), and 1951 (> 1930).



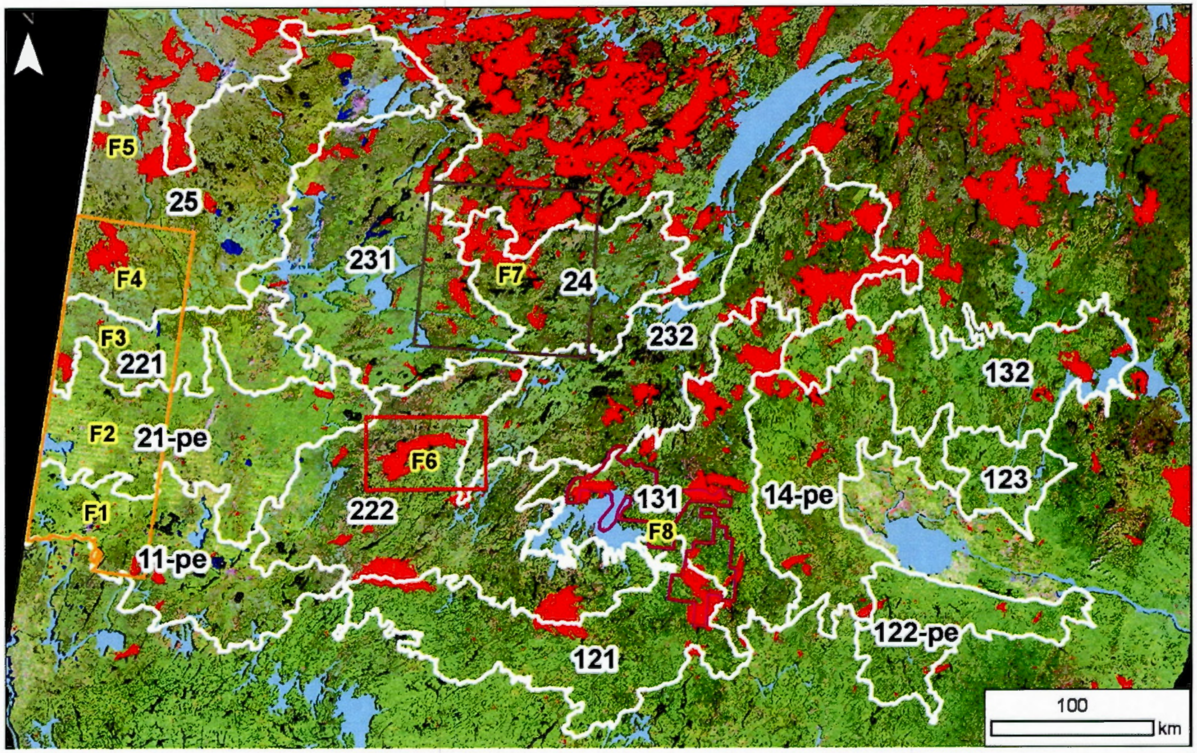


Appendix A2b. Area and year of origin of contemporary fires in the northern central part of the study area defined by Le Goff et al. (2007) (Figure 3.4, F7). Years of origin are synthesized using 4 classes: 1851 (prior to 1870), 1891 (1870 to 1900), 1921 (1901 to 1930) and 1951 (> 1930).

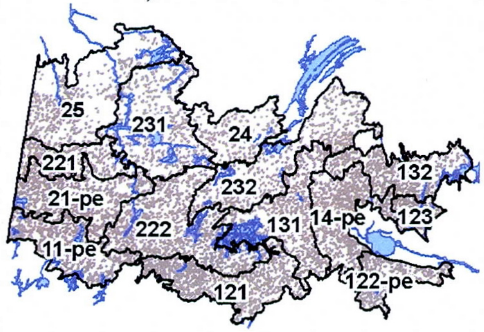




Appendix A2c. Distribution of forest fires (red color) according to data collected between 1971 and 2000 by the MRN. The homogeneous landscape units are delineated in white and described in figure 3.2. Fire origin maps (F1 to F8) used to define a fire cycle (Appendix A1) are shown. F1 to F4 correspond to the Abitibi region described by Bergeron et al. (2001), F5 (Cyr et al. 2009), F6 (Bergeron et al. 2001), F7 (Le Goff et al. 2007) and F8 (Lesieur et al. 2002).



Appendix A3. Distribution of forest inventory plots produced by the *Ministère des Ressources naturelles du Québec* (MRN) and used to define a fire cycle for each homogeneous landscape (HL). The total number of plots is 41961. These plots were produced between 1970 and 1998 and, in each of them, three dominant trees were cored (Pressler borer) to evaluate their age (tree rings counted at the base of the trees or at the DBH). Ages have been grouped into four periods of origin (1851, 1891, 1921, 1951). Plots have also been classified according to their stand evolution (spruce budworm outbreak, fire) and human disturbances. The natural 1851 period is the sum of the relative abundance of plots originating from the 1851 and 1951 periods. In some treatments the 1851 period has been subdivided in two periods : 1851 (1800-1850) and 1751 (before 1800).

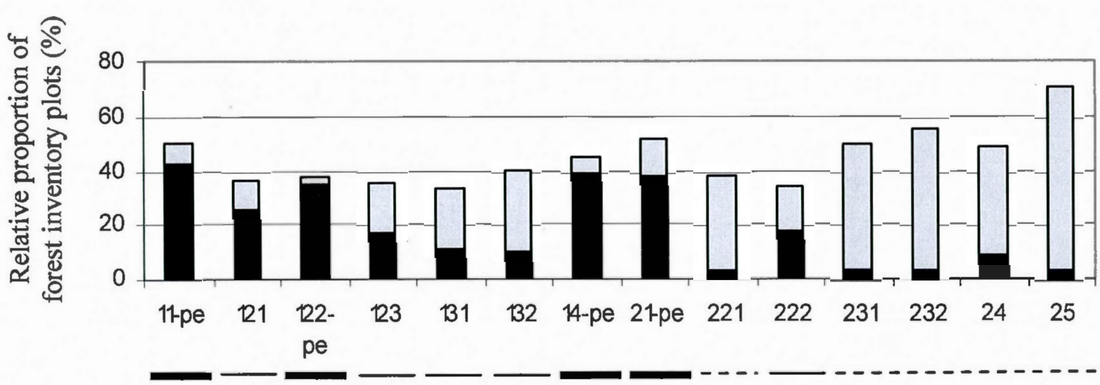


Homogeneous landscape	1851 (1751)	Fire period origin ② 1891	① 1921	③ 1951	1851 (natural)
25	67	14	15	4	71
24	40	17	34	9	49
232	51	24	21	4	56
231	46	20	31	4	50
222	16	25	41	19	35
221	35	14	47	4	39
21-pe	14	9	39	38	52
14-pe	6	21	34	39	45
132	30	33	27	11	41
131	22	31	35	12	33
123	18	25	40	18	35
122-pe	3	11	52	35	37
121	11	23	40	26	37
11-pe	8	14	35	42	51

Homogeneous landscape	Spruce budworm outbreaks 1921o	1891o	1851o	Fires 1921f	1891f	1851f	1751f	④ 1951	⑤ Human fires and logging 1951
25	0	1	4	16	12	42	17	3	0
24	1	2	2	32	15	30	5	9	0
232	3	5	9	23	16	32	8	4	0
231	4	5	8	31	13	29	6	3	0
222	7	6	4	33	23	18	0	13	0
221	3	1	3	45	14	28	3	0	5
21-pe	12	6	5	37	15	19	1	0	14
14-pe	13	7	12	29	15	13	0	0	28
132	10	14	19	14	17	17	2	0	4
131	10	10	8	24	23	16	1	0	10
123	28	18	12	7	6	10	0	0	9
122-pe	38	8	11	14	7	5	1	0	7
121	24	13	11	15	11	11	0	0	11
11-pe	21	7	10	19	12	10	2	0	16

1-2-3-4-5: Data used in table 3.1.

Appendix A4. Relative proportion of forest inventory plots (MRN) belonging to the 1951 and 1851 periods in each homogeneous landscape.



■ 1951 period □ 1851 period

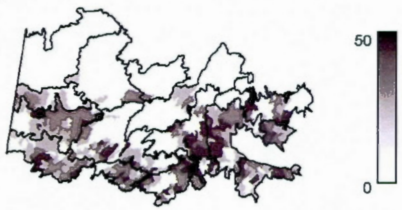
▬ Landscape heavily affected by human activities (*Populus tremuloides* expansion). Landscape 121 is considered as strongly affected by human disturbances in this study. This classification is different from that of Grondin et al. (2014) (Figure 3.2).

— Landscape affected by human activities (logging) but where *Populus* expansion is less pronounced than in previous landscapes

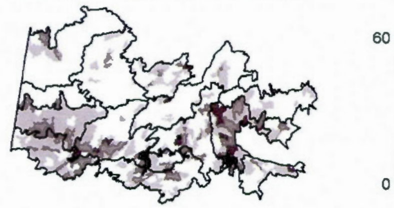
---- Landscape relatively natural according to the data used in this study (forest plots produced during the period 1970-2000)

Appendix A5. Relationship between the distribution and abundance of human activities (logging) and forest inventory plots (MRN) belonging to the 1951 and 1851 periods. On the maps, described with regard to ecological districts, the darker the shade of gray, the

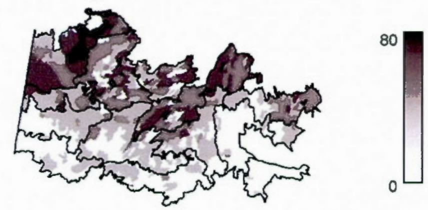
A5a. Distribution and relative abundance of logging during the 1970s period (SIFORT-1)



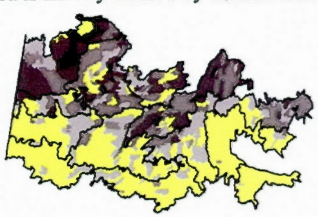
A5b. Distribution and relative abundance of forest plots originating from the 1951 period (> 1930)



A5c. Distribution and relative abundance of forest plots originating from the 1851 period (< 1870), with no adjustment to account for human activities.

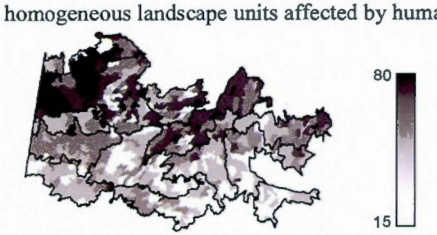


A5d. Distribution of ecological districts (yellow color) characterized by <15% of plots originating from the 1851 period. This low abundance is the southern part of the study area is mainly caused by human activities (logging)

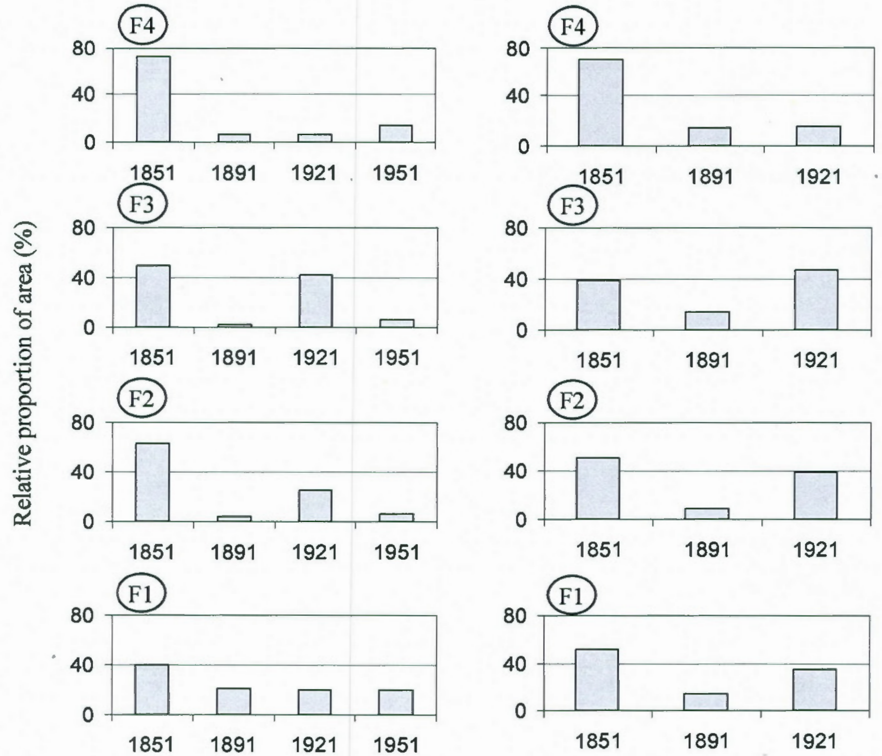


A5e. Mean age of forest plots. In the portions heavily affected by logging, the mean age is less than 75 years

A5f. Relative proportion of plots from the 1851 period (natural 1851 period, see Appendix A3), once the stands of the 1951 period were included in the distribution. This distribution has been used to calculate the fire cycle in the homogeneous landscape units affected by human activities.



Appendix A6. Comparison of age structure histograms of areas studied by Bergeron et al. (2001) (Figure 3.4, F1 to F4). On the left portion, the age structure histograms are defined using the fire origin map created by Bergeron et al. (2001) and, on the right portion, using the MRN forest inventory plots. On the right portion, plots of the 1951 period, mainly originating from human activities, are integrated with those of the 1851 period

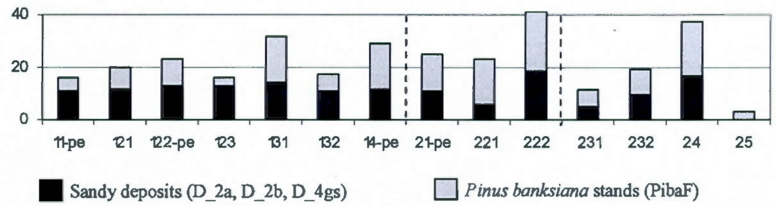


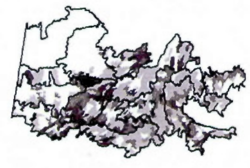
Periods of origin defined by the fire origin map of Bergeron et al. (2001)

Periods of origin defined by the forest inventory plots (MRN-Ministère des Ressources naturelles)

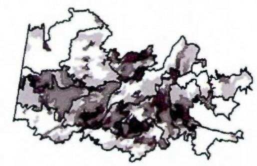
Appendix A7. Distribution and abundance of some forest stands and explanatory variables used to classify the homogeneous landscape units into a specific fire cycle. Links are also established between homogeneous landscapes units and the fire cycle (Figure 3.4, C1, C2, C3). On the maps, the darker the shade of gray, the greater the abundance of the variable. The homogeneous landscape units are outlined (dark lines)

A7a. Relative proportion of *Pinus banksiana* and sandy deposits



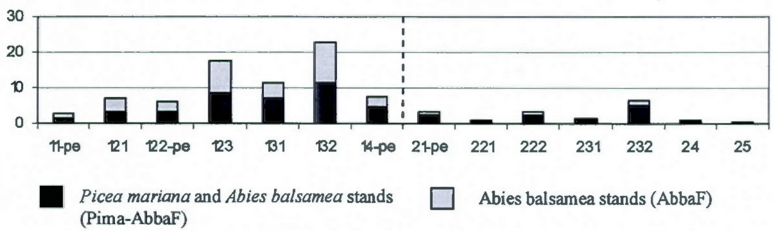


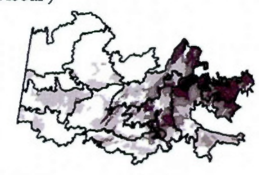
Distribution and relative abundance of sandy deposits according to the description of ecological districts (MRN)



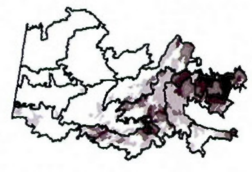
Distribution and relative abundance of *Pinus banksiana* according to forest maps of the 1980s (geobase SIFORT-2).

A7b. Relative proportion of *Picea mariana* and *Abies balsamea* stands (PimaAbbaF) and *Abies balsamea* stands (AbbaF)



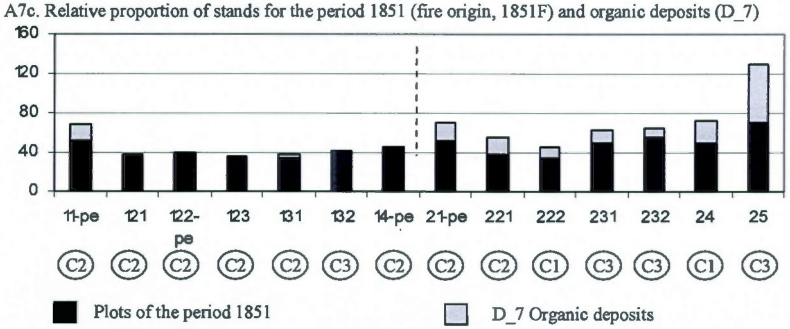


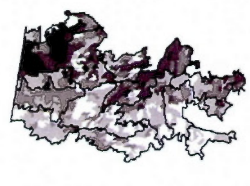
Distribution and relative abundance of *Picea mariana* and *Abies balsamea* forest stands (Pima_AbbaF) (SIFORT-2)



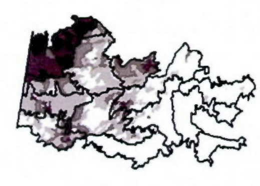
Distribution and relative abundance of *Abies balsamea* forest stands (AbbaF) (SIFORT-2)

A7c. Relative proportion of stands for the period 1851 (fire origin, 1851F) and organic deposits (D_7)



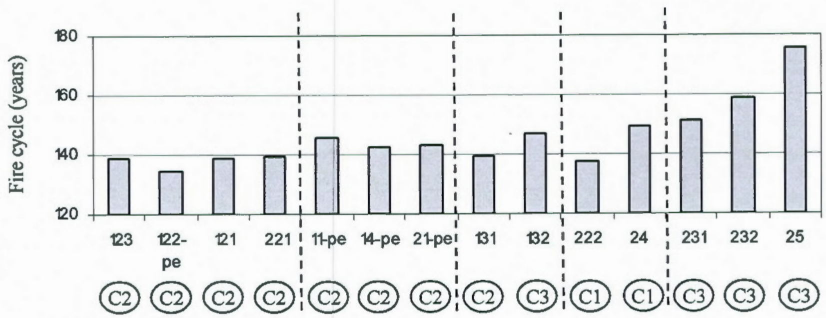


Distribution and relative abundance of stands originating from the 1851 period (natural landscape, see appendix A5f) (MRN forest inventory plots)

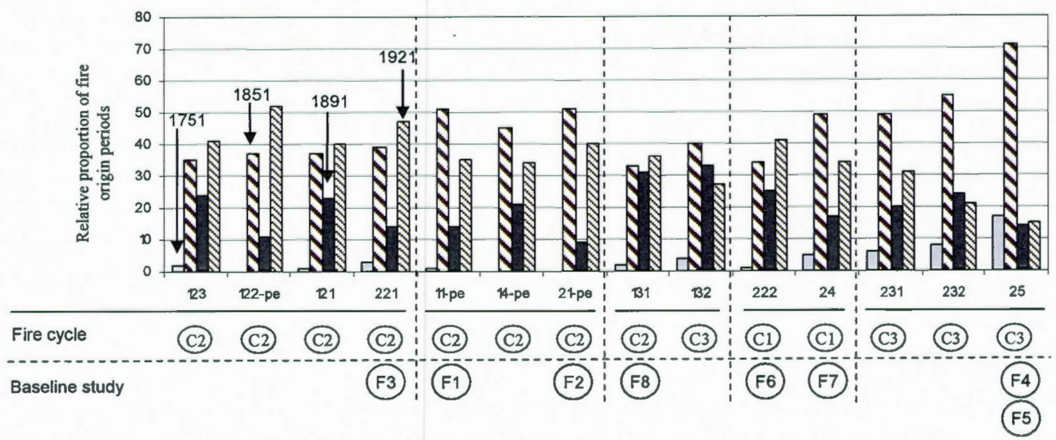


Distribution and relative abundance of organic deposits (D_7) (MRN forest inventory plots)

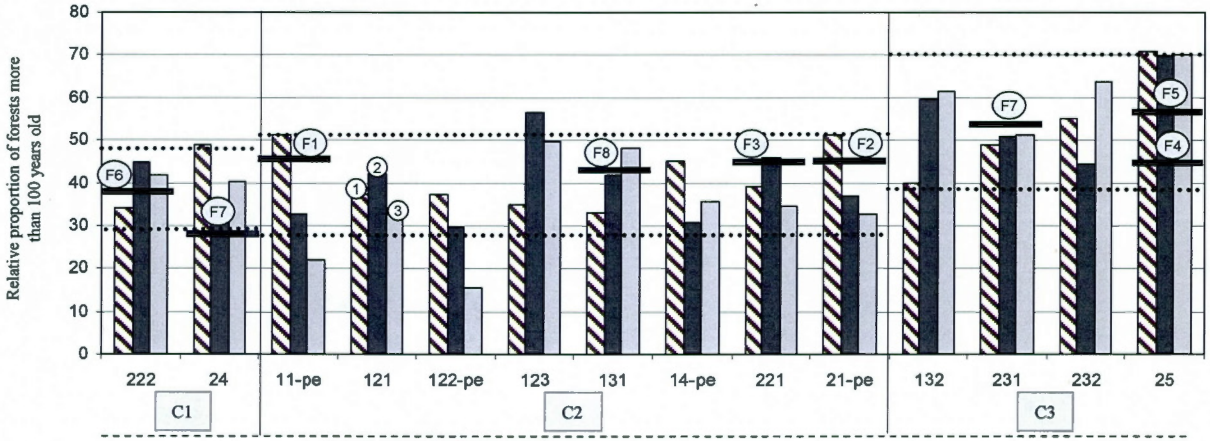
Appendix A8. Fire cycle estimate for each homogeneous landscape unit based on forest inventory plots (MRN). Links are established with fire cycles (Figures 3.4; 3.5)



Appendix A9. Relative proportion of fire origin periods characterizing each homogeneous landscape unit and considering forest inventory plots (MRN). Four periods are considered : 1751 (prior to 1800), 1851 (1800-1870), 1891 (1871 to 1900) and 1921 (>1901). Links are established with fire cycles (Figure 3.4, C1 to C3) and baseline studies (Figure 3.4, Appendix A1, F1 to F8). In a fire cycle of 140 years (C2), the plots of the period 1921 dominate or are slightly dominated by those of the period 1851. In a fire cycle of 180 years or more, the plots of the period 1851 dominate those of the period 1921 by at least 20%.



Appendix A10. Relationship between the proportions of stands more than 100 years old according to baseline studies on fire cycles (F1 to F8) and the proportions defined in other sources of information. The goal of this figure is to define a spatial fire variability in our study area. This variability is inferior to that of the temporal variability. The purpose of this figure is to define a spatial variability of fire cycles in our study area. This variability is less than that of the temporal fire cycle variability (Figure 3.5; Appendix A1).



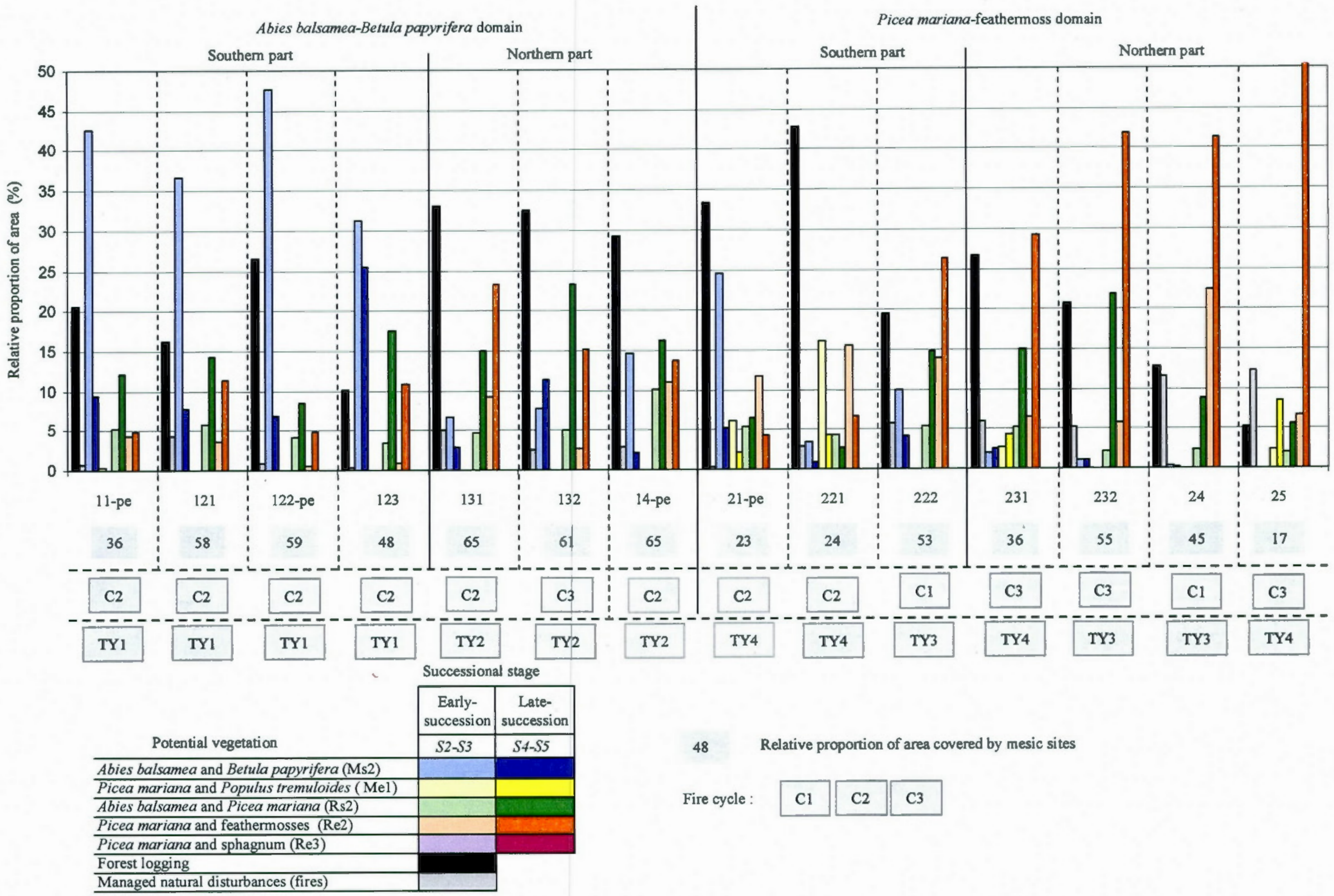
Fire cycle (spatial variability)	Homogeneous landscape unit	Fire cycle - forest inventory plots (Appendix A7)	Proportion of forests more than 100 years old: 1- Plots of the 1851 period	2- Sifort-1 Mature forest	3- Sifort-2, 90-120 years and logging	Fire cycle according to baseline studies	Proportion of old forests according to baseline studies
C1- 110 years (80 à 130)	222	137	34	45	42	111-F6	40
	24	149	49	32	40	85-F7	30
	11-pe	146	51	33	22	139- F1	46
	121	134	37	42	32		
	122-pe	134	37	30	16		
C2- 140 years (80 à 150)	123	134	35	57	50		
	131	139	33	42	48	127-F8	45
	14-pe	147	45	31	36		
	221	140	39	46	35	139- F3	46
	21-pe	143	51	37	32	139- F2	46
	132	147	40	60	62		
C3- 180 years (100 à 220)	231	151	49	51	51	178-F7	54
	232	159	55	44	64		
	25	176	71	70	70	139-F4	46

Sources of information on the proportion of forests more than 100 years old
1- Forest inventory plots (MRN): proportion of stands for the 1851 period (less than 1870)
2- SIFORT-1: proportion of mature forests according to maps produced in the 1970s
3- SIFORT-2: proportion of 90 and 120 years old forest classes and recent logging according to maps produced in the 1980s

F3 Proportion of forests more than 100 years old according to studies specific to fire cycles (Figure 3.4, F1 to F8)

Spatial variability of the forests more than 100 years old

Appendix A11. Description of homogeneous landscape units in relation to their potential vegetation type and successional stages on mesic sites (mainly till), the fire cycle (C1 to C3, Figure 3.4) and the geographical change of forest composition (TY1 to TY4, Figure 3.8). The color codes are provided in figure 3.6. The data comes from the third decennial program of the MRN.



Appendix A12. Equations used to model the age structure (Figure 3.3A2)

Equation A1. Van Wagner distribution used to define the age structure of each homogeneous landscape unit

$$H(u_k, c_k; t) := \begin{cases} \exp(-t/c_k) & \text{for } t \geq 0 \\ 0 & \text{otherwise} \end{cases}$$

H: proportion of area (%) between a specific age class and the end of the distribution;

U:= { $u_1, \dots, u_N$ } : set of homogeneous landscape units u_k;

c_k*:* fire cycle;

t: area of an age class; the age corresponding to the time elapsed since last fire.

Equation A2. Relative proportion of area (%) e_j assigned to each age class

$$e_j(u_k, c_k, I_j) := \begin{cases} \left(1 - H(u_k, c_k; I_j^+)\right) * 100\% & \text{if } j = 1 \\ \left(H(u_k, c_k; I_j^-) - H(u_k, c_k; I_j^+)\right) * 100\% & \text{if } j \geq 2 \end{cases}$$

age classes: I:= { $I_1, \dots, I_N$ }={ [0,10),[10,20),[20,30),[30,40),[40,50) … , [490,500)};

I_j^+ : upper limit, I_j^- : lower limit ;

u_k*:* homogeneous landscape unit;

c_k: fire cycle;

t: age (time elapsed since last fire)

Equation A3. Relative proportion of area (%) w_j adjusted for area exceeding 500 years. The excess area is distributed to the pro rata of age classes

$$w_j(u_k, c_k, I_j) := e_j(u_k, c_k, I_j) / \sum_i e_i(u_k, c_k, I_i) \text{ and } \sum_i w_i(u_k, c_k, I_i) = 100\%$$

Equation A4. Relative proportion of forests more than 100 years old (%) in a homogeneous landscape unit when the fire cycle is known

$$f100 = G(c_k) = \int_{100}^{\infty} \exp(-t/c_k)\,dt * 100\%$$

Equation A5. Fire cycle corresponding to different proportions of forests more than 100 years old

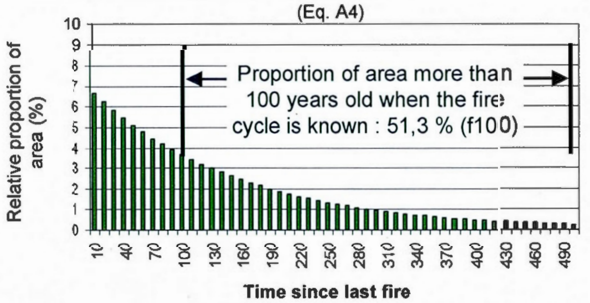
$$c_k = G^{-1}(f100)$$

Appendix A13. Van Wagner model used to describe the age structure of each homogeneous landscape unit

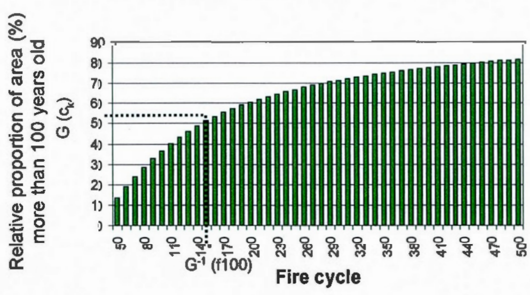
Age structure of a homogeneous landscape unit characterized by a fire cycle of 150 years (c_k = 150 years).

Age class	(Eq. A1) Application of Van Wagner model	(Eq. A2) Proportion of area assigned to each age class	(Eq. A3) Proportion of area (%) adjusted for area exceding 500 years
10	93,551	6,449	6,688
20	87,517	6,033	6,257
30	81,873	5,644	5,853
40	76,593	5,280	5,476
50	71,653	4,940	5,122
60	67,032	4,621	4,792
70	62,709	4,323	4,483
80	58,665	4,044	4,194
90	54,881	3,783	3,923
100	51,342	3,539	3,670
460	4,658	0,321	0,333
470	4,357	0,300	0,311
480	4,076	0,281	0,291
490	3,813	0,263	0,273
500	3,567	0,246	0,255
	Total:	96,4	100,0

(Eq. A4)



(Eq. A5)



G (c_k) : Proportion of forests over 100 years old for a fire cycle c_k

G^{-1} (f100) : Proportion of area more than 100 years old for a fire cycle C_k. For a fire cycle of 150 years, the proportion of area more than 100 years old is 51,3%

APPENDIX B

DETERMINING THE FOREST COMPOSITION FOR EACH HOMOGENEOUS LANDSCAPE UNIT

A summary of the method used to model the natural landscape of each homogeneous unit (n=14) is presented in the main part of this study (Figure 3.8). A more detailed description is provided in this appendix.

1. The modeling of forest dynamics

The forest composition was modeled on the basis of potential vegetation types and successional stages (Appendix B1). The classification of each forest inventory plot according to a potential vegetation type was done mainly on the basis of forest species. Keys used to define the potential vegetation are presented in the ecological guides produced by the Ministère des ressources naturelles du Québec (MRN) (e.g. Grondin et al., 2007; Saucier et al., 2009). To standardize the information noted in forest inventory plots over several years, each plot was subjected to a similar key to that presented in Appendix B2. To model forest composition, each plot classified as natural (absence of recent logging) was assigned to a potential vegetation type noted as v_k. All the potential vegetation types form the set V: = {Ms2, Me1, Rs2, Re2, Re3}. A successional stage, denoted as s_k, was also assigned to each plot. All the successional stages compose the set S: = {S2 , S3, S4, S5}. A maximum age a_k corresponding to the oldest tree measured (usually 3 in number) completes the description of each plot. Each forest inventory plot was denoted as $p_k = (v_k, s_k, a_k)$, belonging to a set named P. The set P, defined by all plots without recent human activities, was partitioned in P_m matrices, each described by p_k plots belonging to a specific potential vegetation type (v_k) and to a specific successional stage (s_k) (e.g. Re2-S2). The total number of P_m matrices is 20.

A three-parameter Weibull equation was estimated according to the maximum likelihood (MLE) for each P_m matrix using the F distribution function (Appendices B3 and B4, eq. B6). This equation estimates the values for parameters λ, σ and θ. These parameters were used to create a distribution of area by age class t. Each value of F corresponds to the proportion of area occupied between a specific age class t and the start of the distribution (beginning with the 30 year age class). Equation B7 (Appendices B3 and B4) was used to evaluate the proportion of area d_j attributed to each age class I_j (e.g. 10 years) and each P_m partition (Appendix B4). The minimum age of the Weibull distribution was fixed at 30 years because the minimum age dispersion of P_m (e.g. Ms2-S2) generally varies from 15 to 25 years. The Weibull parameters considered in this study comprise the Appendix B5.

The proportion of the area between the minimum age (10 years) to 30 years is entirely attributed to the class of 30 years class and this proportion is generally 100% for ages less than 350 years. Equation B8 (Appendices B3, B4) was used to evaluate the proportions of areas by age class I_j (e.g. 10 years) and P_m partitions (e.g. Re2-S2). These proportions (PC) by age class (I_j), potential vegetation (v) and successional stage (s) were noted as PCI_{jvs}. Appendix B4 shows an example of the Re2 potential vegetation.

2. Forest dynamics

In the main text describing this study, we briefly discuss the forest dynamics of the potential vegetation types observed in the study area. More details are presented in this appendix. The model of *Abies-Betula* potential vegetation (Ms2, Figure 3.6, Appendix B1) is consistent with the forest successional dynamic described by many authors, including Damman (1964), Carleton and Maycock (1978), Bergeron (2000), Lesieur et al. (2002), Gauthier et al. (2004, 2010), and Couillard et al. (2012). Early-successional species (S2, S3) dominate the landscape before being gradually replaced by late-successional species (S4, S5). This dynamic does not exclude a cyclic dynamic of early-successional stands (*Betula papyrifera* dominance) and also of the late-successional stands, dominated by *Abies balsamea* and vulnerable to insect outbreaks.

The type of potential vegetation classified as *Picea-Populus* (Me1, Figure 3.6, Appendix B1) is characterized by forest types dominated by *Populus tremuloides* (stage S2), *Populus tremuloides* and *Picea mariana* (S3), *Picea mariana* and *Populus tremuloides* (S4), and *Picea mariana* interspersed with some *Abies balsamea* and *Populus tremuloides* (S5). A great diversity of undergrowth species characterizes the stands dominated by *Populus tremuloides*; *Alnus spp.* (*crispa and rugosa*) and herbaceous species dominate. The stands formed principally by *Picea mariana* have a very dense forest cover and an undergrowth dominated by feathermosses. Ericaceous species are present but generally not abundant. The negative exponential of S2 forest stands and the dynamics of other successional stages suggest a successional dynamic from *Populus tremuloides* stands to *Picea mariana* forest stands (Lecomte and Bergeron, 2005). However, a cyclic dynamic could characterize each of the successional stages (Carleton and Maycock, 1978; Gauthier et al., 2004; Arbour and Bergeron, 2011). For example, *Populus tremuloides* stands (S2) could persist after fire, without evolving to the subsequent stages over time. It is also possible for *Populus tremuloides* stands with poor coniferous species regeneration to open into shrubby vegetation dominated by *Alnus spp. (crispa* and *rugosa).* In addition, the proportion of the *Populus tremuloides* stands used in the modeling is probably overestimated compared to the natural situation because of human-caused fires that occurred during the 1880-1940 period in the southwestern portion of the territory. Many of these old fires are not considered as human activities and are used to model the forest dynamic because it was impossible to know the exact origin of each plot. Finally, a portion of late-successional *Picea mariana* stands (or *Picea mariana*) could be subject to paludification (successional paludification). This process was integrated with the model of *Picea mariana*-sphagnum potential vegetation when the thickness of the organic matter exceeded 40 cm (Heinselman, 1981; Lecomte and Bergeron, 2005; Simard et al., 2007). Finally, the model of *Picea-Populus* could have been presented with respect to two pathways. The first starting from *Populus tremuloides* as an early successional stage and the second starting with *Picea mariana* stand, also as early succession. Each of these two pathways could evolved towards stands dominated by *Picea mariana* and *Abies balsamea*.

The model of *Abies-Picea* potential vegetation type (Rs2, Figure 3.6, Appendix B1) has certain similarities with Abies-Betula (Ms2) potential vegetation. As with *Abies-Betula* (Ms2), the *Abies-Picea* (Rs2) potential vegetation seems mainly related to a successional dynamic (as opposed to a cyclic dynamic). This is consistent with the observations of Carleton and Maycock (1978), Bouchard et al. (2008), and Gauthier et al. (2010). Early-successional stands (S2-S3) were dominated by *Betula papyrifera* and those of late-successional stands (S4-S5) by *Abies balsamea* and *Picea mariana*. Sometimes, and essentially in the lower part of the hills, *Picea mariana,* dominated after fire with *Abies balsamea* gradually becoming more and more abundant. As in the *Picea-Populus* (Me1) potential vegetation, two pathways could have been defined.

Modeling *Picea*-feathermoss stands (Re2, Figure 3.6, Appendix B1) suggests a successional dynamic from *Pinus banksiana* (S2) to *Picea mariana* (S5) (Dix and Swan, 1971; Carleton and Maycock, 1978; Cogbill, 1985; Lesieur et al., 2002; Lecomte and Bergeron, 2005). Fires can also initiate a cyclic dynamic of *Pinus banksiana* (Harper et al., 2002) and even *Picea mariana* (Dix and Swan, 1971; Cogbill, 1985; DeGrandpré et al., 2000; Gauthier et al., 2010). The cyclic dynamic of *Pinus banksiana* is more frequent on coarse deposits (Shafi and Yarranton, 1973). With increasing time since the last fire, the late successional stands (*Picea mariana*) located on relatively flat topography and characterized by a thick layer of organic soils can be associated with the paludification process, which causes lower productivity and opening of forest stands (Lecomte et al., 2005; Simard et al., 2007). The sites affected by paludification were classified with the *Picea*-sphagnum (Re3) potential vegetation. In other cases, on mesic to xeric soils. *Picea mariana*-feathermoss stands are characterized by forest opening after fire and the formation of *Picea mariana*-lichens formations. These situations are relatively rare in our study area and were not considered in the model (Girard et al., 2008).

The modeling of the *Picea*-sphagnum potential vegetation (Re3, Figure 3.6, Appendix B6) was characterized mainly by *Larix laricina* (stage S2), *Larix laricina*-*Picea mariana* (S3), *Picea mariana-Larix laricina* (S4), and *Picea mariana* (S5) forest stands. The successional dynamic seems to be supported by most authors (Carleton and Maycock, 1978; Cogbill, 1985; Gauthier et al., 2000; Lecomte and Bergeron, 2005). Regardless of fire severity, these ecosystems are characterized by a thick layer of organic material (more than 40 cm, edaphic paludification Simard et al., 2007) and a low productivity.

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Grondin, P., Berger, J.-P., Landry, Y., Leboeuf, P., 2007. Guide de reconnaissance des types écologiques des régions écologiques 5j – Île d'Anticosti et îles de Mingan de même que 5k – Îles de la Madeleine, Québec, Division de l'analyse et de la diffusion des informations forestières et écologiques, Direction des inventaires forestiers, Ministère des Ressources naturelles et de la Faune, Forêt Québec.

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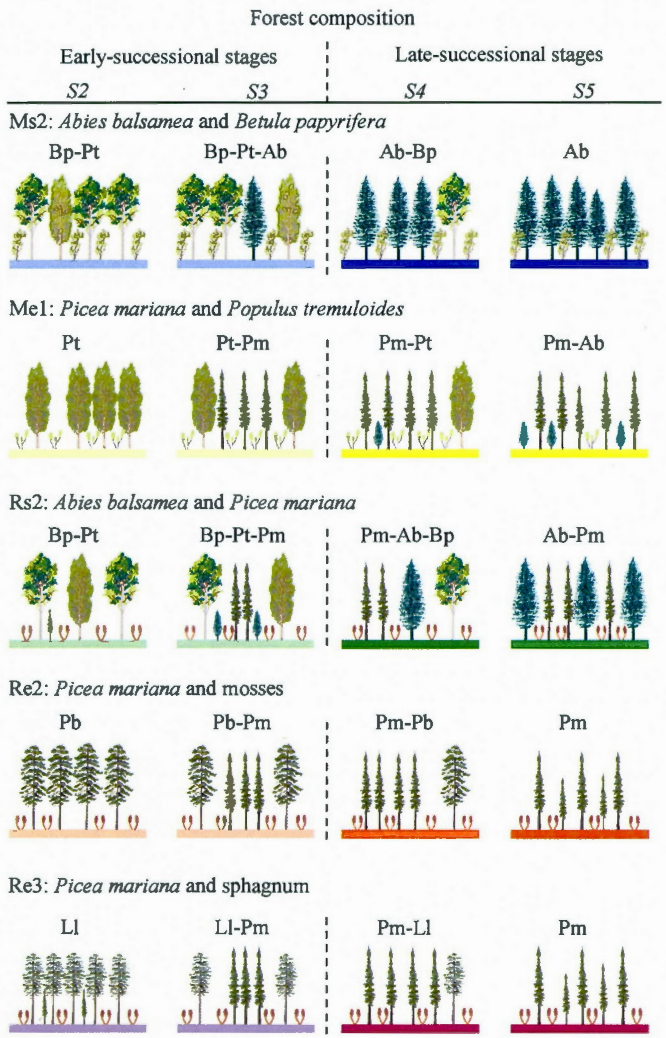
3. Describing homogeneous landscape units in relation to their age structure and forest dynamics

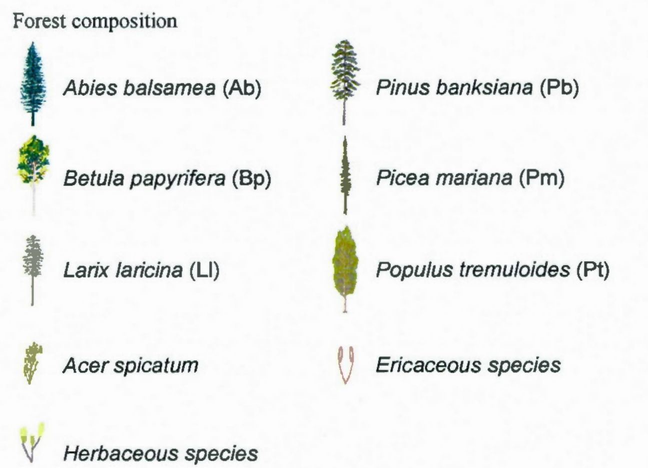
The definition of the modeled natural landscape of each homogeneous landscape unit according to their age and their composition consists in the integration of age structure and forest dynamic modeling (Figure 3.3). The age structure is derived from the Van Wagner distribution (Van Wagner, 1978) (Appendices A12, A13). The forest dynamic modeling is based on the Weibull distribution applied on a relative proportion of area by age classes defined by potential vegetation and successional stages (Appendices B3, B4, B6). The combination of the age structure and forest dynamic is achieved through two weightings (P1 and P2) (Appendices B3, B6). The first (P1) consists of using the proportions of areas defined in the previous step by potential vegetation types and successional stages (PCI_{jvs}) and multiplying them by the proportions of areas w_{jk} (u_k, c_k, I_j) determined by the Van Wagner model (Van Wagner, 1978). This integration is formulated by the equation B9 (Appendix B3). An example is given in the appendix B6.

A second weighting is introduced to measure the relative proportion of all potential vegetation types and successional stages defined for each homogeneous landscape unit (Appendix B3, eq. B10, example in appendix B6). This equation takes into account the area covered by the various potential vegetation types in each homogeneous landscape unit. These areas are defined by SIFORT-2 forest maps that were developed by the MRN during the 1980's.

Van Wagner, C.E., 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res. 8, 220–227.

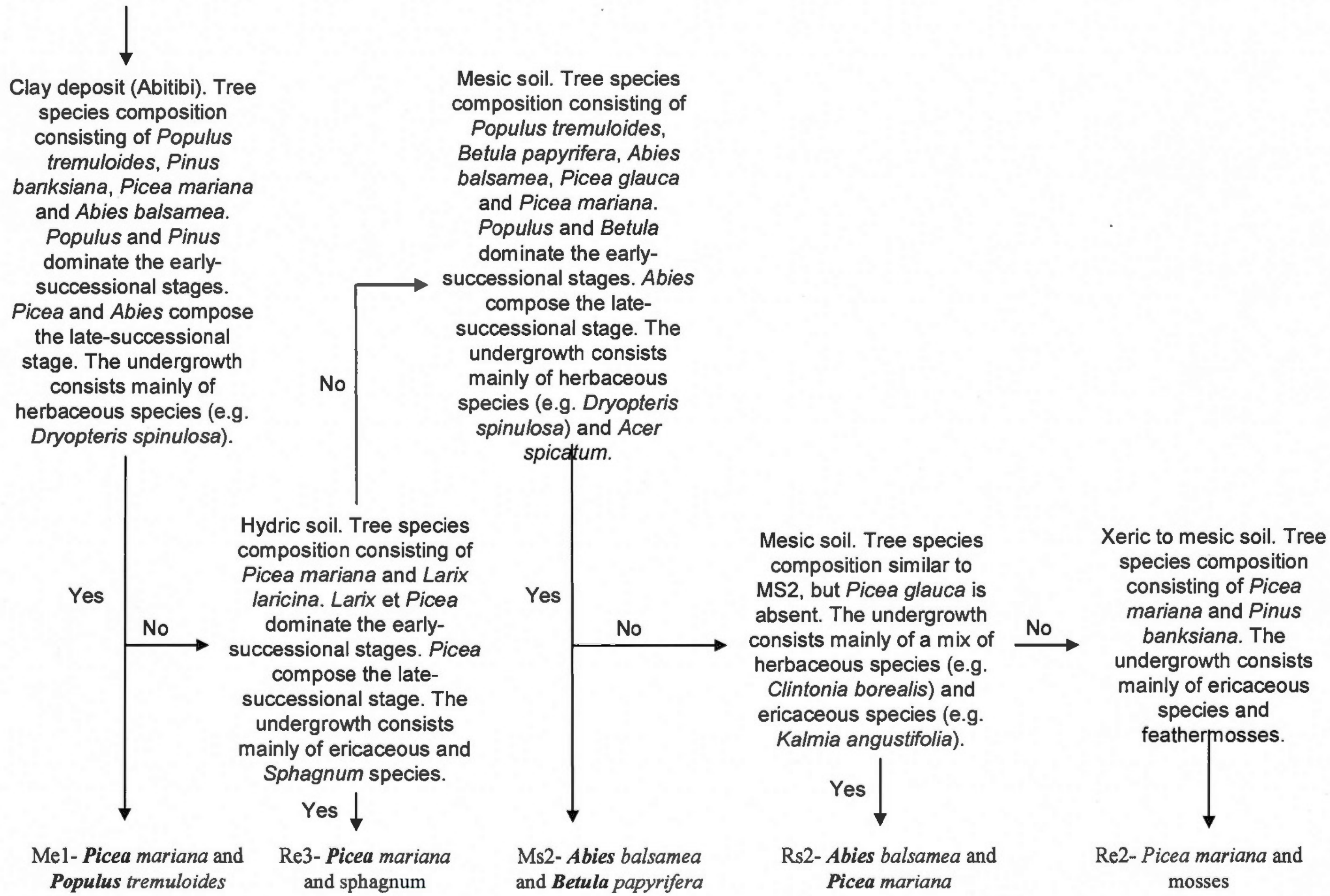
Appendix B1. Potential vegetation and successional stages considered in this study





	Successional stage	
	Early-succession	Late-succession
Potential vegetation	*S2-S3*	*S4-S5*
Abies *balsamea* and ***Betula*** *papyrifera* (Ms2)		
Picea *mariana* and ***Populus*** *tremuloides* (Me1)		
Abies *balsamea* and ***Picea*** *mariana* (Rs2)		
Picea *mariana* and mosses (Re2)		
Picea *mariana* and sphagnum (Re3)		

Appendix B2. Synthetic key for the identification of potential vegetation types considered in this study



Appendix B3. Equations used to model forest composition (Figure 3.3A3)

Equation B6 Weibull model used to describe the forest composition of each combination of potential vegetation type and successional stages (n = 20).

$$F(\lambda_m, \sigma_m, \theta_m; t) := \begin{cases} 1 - \exp(-(\frac{t-\theta}{\sigma})^{\lambda}) & \text{if } t \geq \theta \geq 0 \\ 0 & \text{otherwise} \end{cases}$$

F: proportion by age class (%);

λ_m : parameter associated with the form of the age distribution a_{jm} of each partition Pm ;

σ_m : parameter expressing the age distribution a_{jm} of each partition Pm;

θ_m : location parameter associated with the minimum age of each partition Pm;

t: age class (time elapsed since last fire).

Equation B7 Relative proportion of area (%) (d_j) assigned to each age class I_j

$$d_j(v,s,I_j) := \begin{cases} \left(F(\lambda_m, \sigma_m, \theta_m; I_j^+) - F(\lambda_m, \sigma_m, \theta_m; I_j^-)\right) * 100\% & \text{si}\, \theta_m \leq I_j^- \\ \left(F(\lambda_m, \sigma_m, \theta_m; I_j^+)\right) * 100\% & \text{si}\, I_j^- \leq \theta_m < I_j^+ \\ 0 & \text{si}\, I_j^+ < \theta_m \end{cases}$$

age classes: I:= { $I_1, \ldots , I_N$ }={ [0,30),[30,40),[40,50) … ,[490,500)};

I_j^+ : upper limit, I_j^- : lower limit of age class.

Equation B8 Proportion of area by age class

$$PC1_{k\tilde{v}s} := 100 * \frac{d_j(\tilde{v}, s, I_k)}{\sum_{s \in S} d_j(\tilde{v}, s, I_k)} \text{ noting that } \sum_{s \in S} PC1_{k\tilde{v}s} = 100$$

Integration of age structure and forest modeling (Figure 3.3A4, 3.3A5, Appendix B6)

Equation B9 First weighting of the proportion of area by age class and considering each potential vegetation type for a specific homogeneous landscape

$$P1_{k\tilde{v}s} := \frac{PC1_{k\tilde{v}s} * w_k}{100} \text{ noting that } w_k = \sum_{s \in S} P1_{k\tilde{v}s}$$

Equation B10 Second weighting of the proportion of area by age class and considering all potential vegetation types for a specific homogeneous landscape

$$P2_{k\tilde{v}s} := P1_{k\tilde{v}s} \frac{surf(\tilde{v})}{surf(u_k)} \text{ noting that } \sum_k \sum_{s \in S} \sum_{v \in V} P2_{kvs} = 100\%$$

Appendix B4. Weibull model used to describe the forest dynamics of potential vegetation types and successional stages

A. Pm matrices for the potential vegetation Re2 (Re2-S2, Re2-S3, Re2-S4, Re2-S5)

Plot number	Potential vegetation	Successional stage	Age
2195	Re2	S2	75
2119	Re2	S2	87
2275	Re2	S3	133

B. Weibull parameters according to the four Pm matrices forming potential vegetation Re2

		(Eq. 6)		
Potential vegetation	Successional stage	λ	σ	θ
Re2	*S2*	3.0149	69	8
	S3	3.1076	75	17
	S4	2.8311	88	12
	S5	2.4326	122	14

C. Weibull model applied to the combination Re2-*S2* (age class from 30 to 500 years).

	a	b (Eq. B6)	c (Eq. B7)	d (Eq. B8)
Age class	Re2_TOT	Re2,*S2*	Re2,*S2*_S	Re2,*S2*_PC
30	5.608	3.300	3.277	58.441
40	12.802	9.600	6.348	49.589
50	23.496	20.300	10.723	45.637
60	34.884	35.000	14.635	41.954

a. Total proportion of plots for all successional stages (S2, S3, S4, S5) of Re2 potential vegetation

b. For the combination Re2-S2 : proportion (3.3 %) of the distribution between the minimum age distribution (θ) and the upper limit of a specific age

c. For the combination Re2-S2 : proportion (3.3 %) of the age class between the minimal age (8 years) and 30 years 6.3 % : proportion between 30 and 40 years (9.6-3.3)

d. For the combination Re2-S2 : Proportion of plots (%) by age class. The proportion 3.3% represents 58% of the total proportion of Re2 at 30 years (Re2_tot) ((3.3/5.6)*100) = 58 %

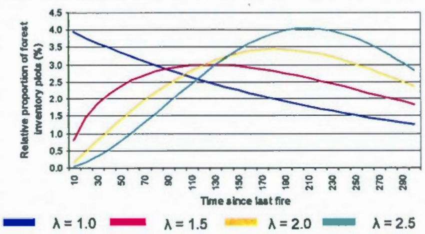
D. The proportion of area of all successional stages of potential vegetation Re2 (Eq. B8).

Age class	d Re2,*S2*_PC	Re2,*S3*_PC	Re2,*S4*_PC	e Re2,*S5*_PC
30	58.441	7.874	20.520	13.165
40	49.589	16.304	21.538	12.569
50	45.637	21.217	21.552	11.594
60	41.954	25.000	21.840	11.206

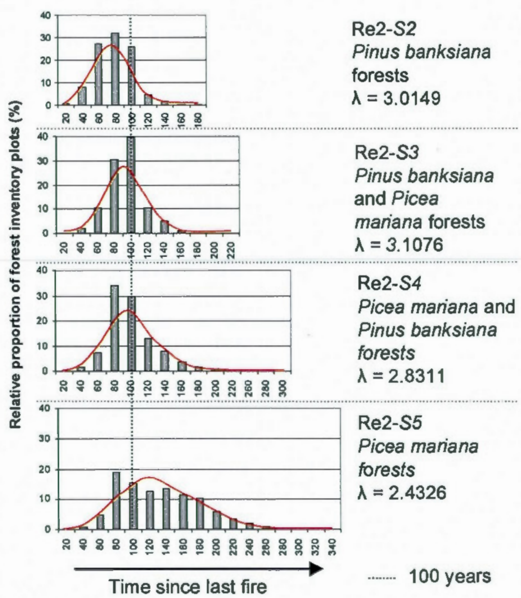
d. Proportion of area for Re2-S2

e. Proportion of area for Re2-S5

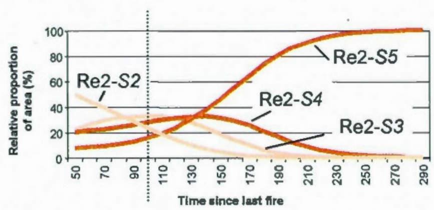
E. Forest dynamics modeling. The parameter λ defines the form of the Weibull distribution. When the value is close to 2.5, the curve is similar to a normal distribution.



F. The model (red line), developed from the potential vegetation and successional stages is adjusted to the relative proportions of age classes defined by forest inventory plots. The example is for potential vegetation Re2



G. Forest modeling of Re2 potential vegetation developed using all of the forest plots forming the potential vegetation of the study area.



The relative proportion of plots characterizing Re2-*S2* decreases gradually with age to the benefit of Re2-*S5*. Considering the large number of forest inventory plots, the frequency of plots is interpreted as relative area.

Appendix B5. Descriptive and statistical data related to the modeling of forest dynamics by potential vegetation type and successional stage. Potential vegetation types and successional stages are defined in appendix B1

Potential vegetation	Sussessional stage	Number of plots	Weibull parameters		
			λ	σ	θ
Me1	*S2*	679	1.83	40	25
	S3	122	2.28	53	24
	S4	106	2.20	58	25
	S5	69	2.30	67	27
Ms2	*S2*	2838	2.25	70	10
	S3	1963	2.24	74	15
	S4	1949	2.43	80	13
	S5	1696	2.04	81	16
Re2	*S2*	1462	3.01	69	8
	S3	2246	3.11	75	17
	S4	3161	2.83	88	12
	S5	10907	2.43	122	14
Re3	*S2*	20	2.17	86	8
	S3	51	1.55	58	35
	S4	249	1.63	60	38
	S5	2190	2.36	121	27
Rs2	*S2*	1072	2.37	66	16
	S3	1132	2.32	74	18
	S4	2283	2.33	81	16
	S5	4381	2.12	102	15
		38576			

Weibull parameters

λ : parameter associated with the form of the age distribution

σ : parameter expressing the age distribution

θ : location parameter associated with the minimum age of the partition

Appendix B6. Integration of age structure and forest dynamics to describe the natural landscape of each homogeneous landscape unit and comparison with the managed landscape

A. Van Wagner model used with the fire cycle (average age of forests) specific to each homogeneous landscape unit. Example for determining the area covered by Re2-S5

	Eq. A1	Eq. A2	Eq. A3	Eq. B8	Eq. B9	Eq. B10
Age class	e	f	g	e	h	i
30	81,982	18,018	18,700	13,165	2,462	0,323
40	76,728	5,253	5,452	12,569	0,685	0,090
50	71,812	4,917	5,103	11,594	0,592	0,078
60	67,210	4,602	4,776	11,206	0,535	0,070
-						
500	3,647	0,250	0,259	100,000	0,259	0,034
					Total:	6,057

Van Wagner

e Area (%) ≥ to the age class, (Eq. A2.1)

f Area (%) of the age class, (Eq. A2.2)

g Area (%) on a pro rata basis, (Eq. A2.3)

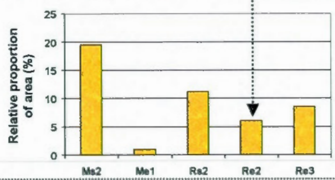
Weibull

e Re2-*S5*_pc (PC, Éq. B2.8)

h Re2-*S5*_p1, Éq. B2.9) (first weighting)

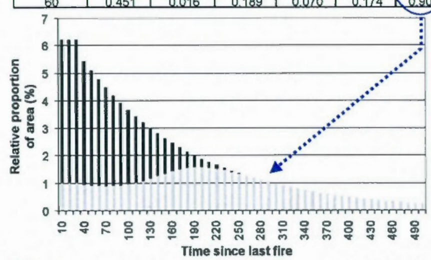
i Re2,*S5*_p2, Éq. B2.10) (second weighting)

B. Modeled natural landscape according to forest composition. Example of the successional stage (S5) for the five potential vegetations in the homogeneous landscape unit under study.



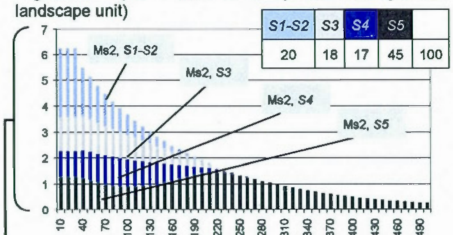
C. Modeled natural landscape according to forest composition and age classes.

Age class	Ms2-*S5*	Me1-*S5*	Rs2-*S5*	Re2-*S5* (i)	Re3-*S5*	TOT_*S5* (j)
10	0.549	0.003	0.355	0.108	0.002	1.018
20	0.549	0.003	0.355	0.108	0.002	1.018
30	0.549	0.003	0.355	0.108	0.002	1.018
40	0.528	0.010	0.240	0.090	0.068	0.936
50	0.486	0.013	0.207	0.078	0.132	0.916
60	0.451	0.016	0.189	0.070	0.174	0.900

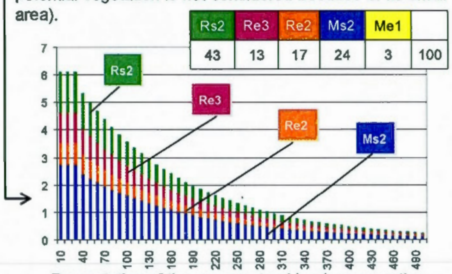


j The area of classes of 10 to 30 years is divided into three equal parts

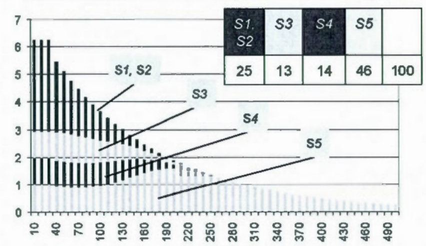
P1: First weighting : Proportions of area distributed according to successional stages of the same potential vegetation (ex. : Ms2 of a specific homogeneous landscape unit)



P2: Second weighting : Proportions of area distributed according to all potential vegetations and successional stages of a specific homogeneous landscape (Me1 potential vegetation is not considered because of its small area).

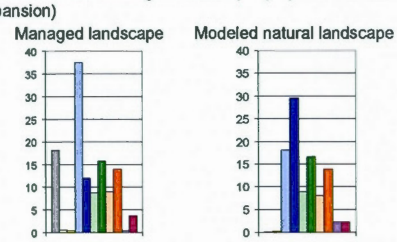


Presentation of the same natural landscape as the previous one, but considering successional stages



Time since last fire

Comparison between the managed and the modeled natural landscape of a specific homogeneous landscape. Ms2-S2 is abundant in the managed landscape (*Populus tremuloides* expansion)



	Ms2, *S2-S3*	Ms2, *S4-S5*	Total
Modeled natural landscape	18 %	30 %	48 %
Managed landscape	37 %	11 %	48 %

APPENDIX C

COMPARING NATURAL AND MANAGED LANDSCAPES IN TERMS OF FOREST COMPOSITION AND AGE STRUCTURE

Natural landscapes defined by the combination of fire cycles and modeling of forest dynamics were compared to managed landscapes. To simplify the presentation of results (Figures 3.7, 3.8, 3.9), only a few homogeneous landscape units have been described (121, 14-pe, 222, 231). Appendices C1a and C1b compares all homogeneous landscape units on the basis of their estimated natural and managed landscapes. The appendix demonstrates the homogeneity of the landscapes in each type of composition (TY1, TY2, TY3, TY4).

- Landscape 121 is representative of all the landscapes associated with the first type of composition change (TY1). In the four landscapes composing TY1, potential vegetation *Abies-Betula* (Ms2) dominates (southern part of the *Abies Balsamea-Betula papyrifera* domain) (Figure 3.2). The late successional stages forming each potential vegetation are always more abundant than early successional stages. In managed landscapes, *Abies-Betula* early stages (Ms2-S2S3) are always more abundant than *Abies-Betula* late stages (Ms2-S4S5).

- Landscape 14-pe is representative of all the landscapes associated to the second type of composition (TY2). In the three landscapes composing TY2, potential vegetation types *Abies-Picea* (Rs2) and *Picea*-mosses (Re2) dominate (northern part of the *Abies Balsamea-Betula papyrifera* domain). The late successional stages forming each potential vegetation types are always more abundant than early successional stages. In managed landscapes, logging is abundant and all successional stages are less abundant than in natural landscapes. The logging is relatively recent and the response of vegetation to human activities will become apparent only after a number of years. We expect that the changes will be less notable than in *Abies-Betula* (Ms2) potential vegetation. Relatively intensive silviculture (coniferous species plantation) would also contribute to diminishing the differences between the two landscape types.

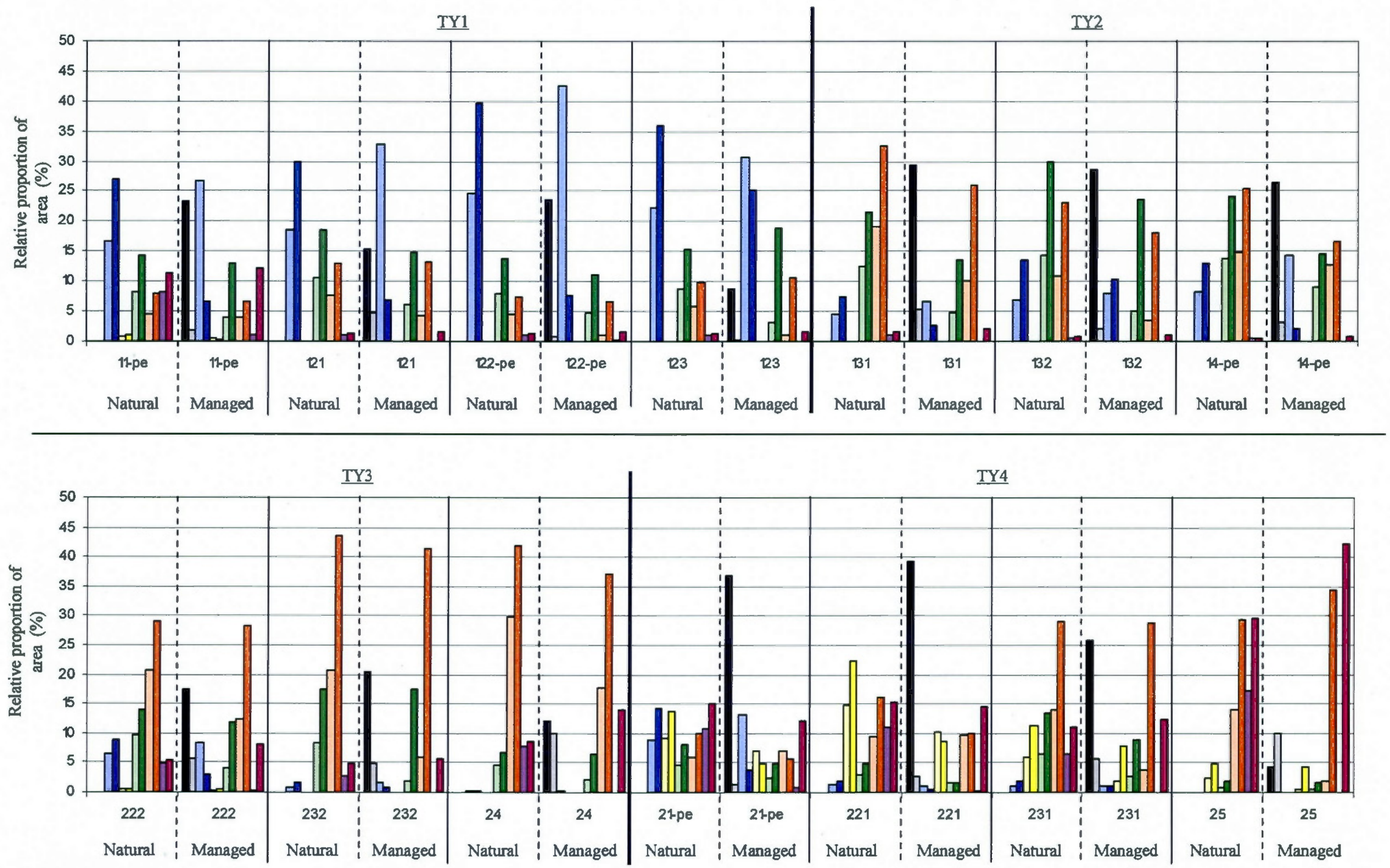
- Landscape 222 is representative of all the landscapes associated with the third type of composition (TY3). In the three landscapes composing TY3, potential vegetation *Picea*-mosses (Re2) dominates. The late successional stages forming each potential vegetation are always more abundant than early successional stages. Early successional stages of *Picea*-mosses (Re2) potential vegetation are very abundant in 24. This proportion is related to sandy deposits (Appendix A7a).

- Landscape 231 is representative of all the landscapes associated to the fourth type of composition (TY4). In the three landscapes composing TY4, there is a large variety of potential vegetation and successional stages. The proportions of early successional stages of *Picea*-mosses (Re2-S2S3) are always well represented in the natural landscape. To correct this situation it would be necessary to increase the fire cycle.

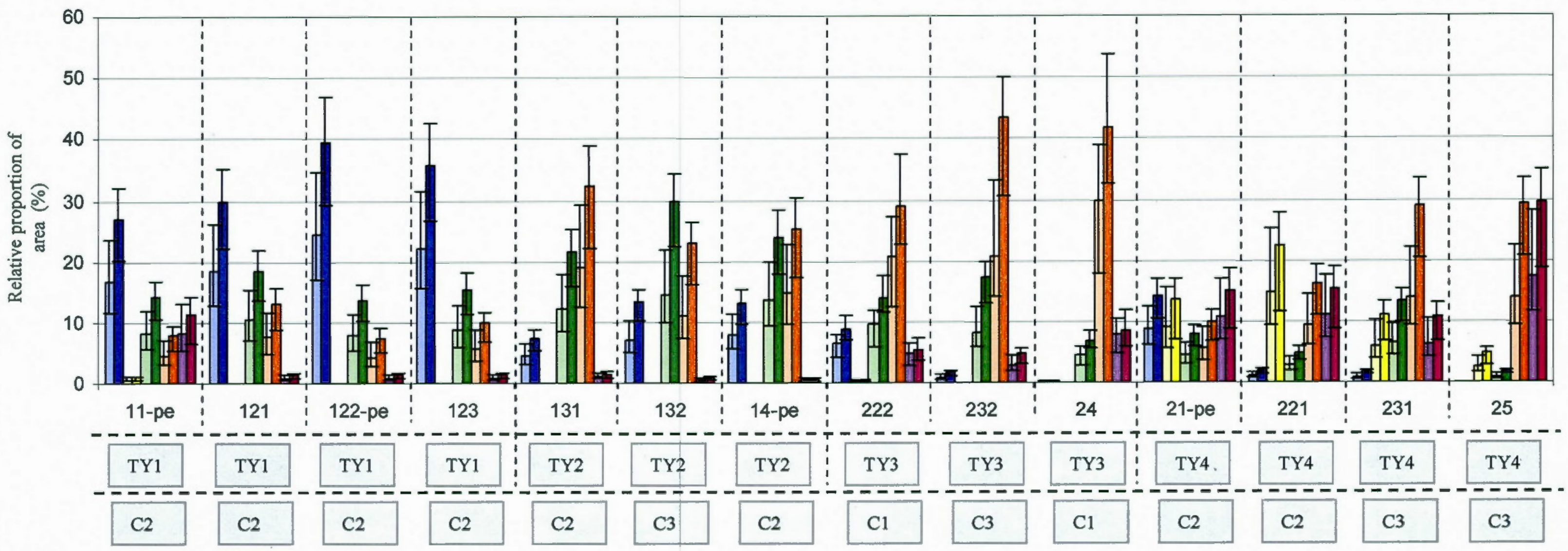
Appendix C2 also compares the natural and managed landscapes. While this comparison is limited to a few landscapes but it does takes logging into account. Natural landscapes without logging have been created by redistributing the area affected by human activities to the potential vegetation and successional stages dominated by coniferous species.

Appendix C3 compares the age structure of the 14 homogeneous landscapes. This appendix is a complement to the figure 3.9.

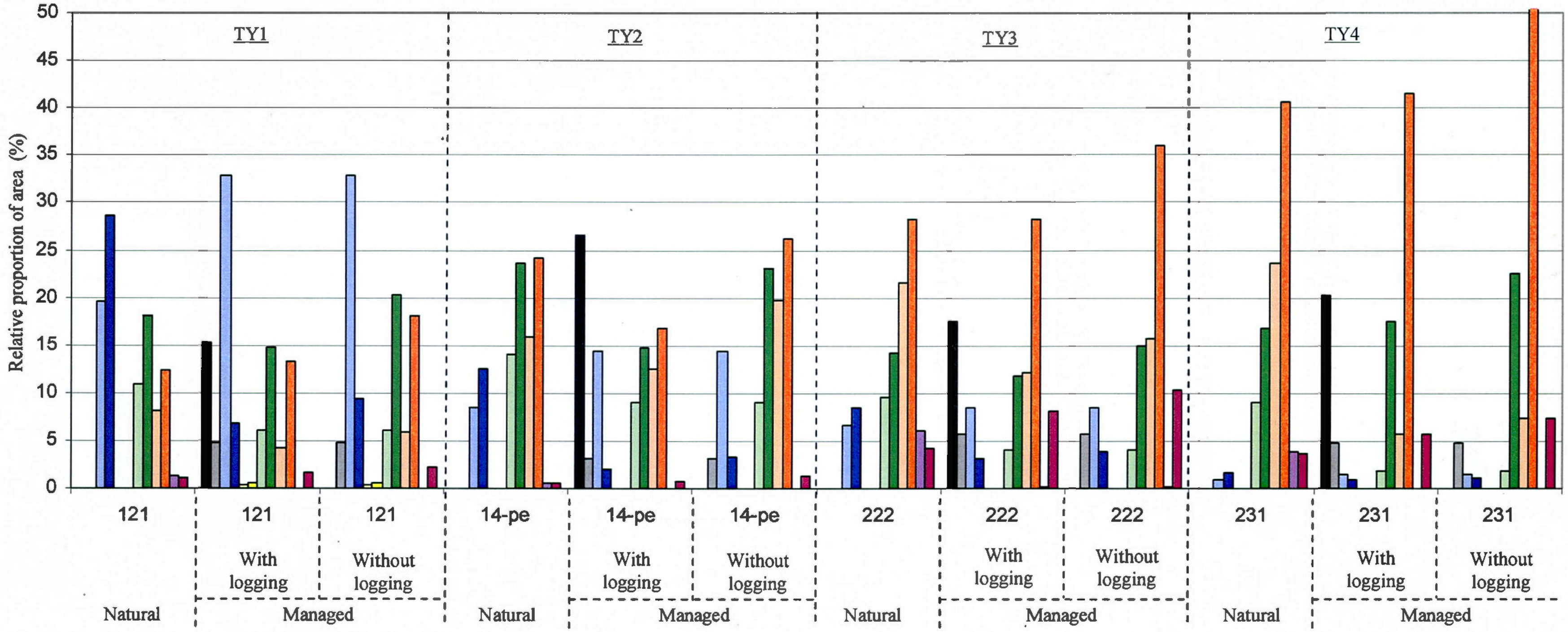
Appendix C1a. Comparison of modeled natural landscapes and managed landscapes on the basis of four geographical types of forest composition (TY1 to TY4) and the combination of potential vegetation types and successional stages characterizing each of the 14 homogeneous landscape units. The color codes are provided in figure 3.8. Logging is considered in the description of managed landscapes.



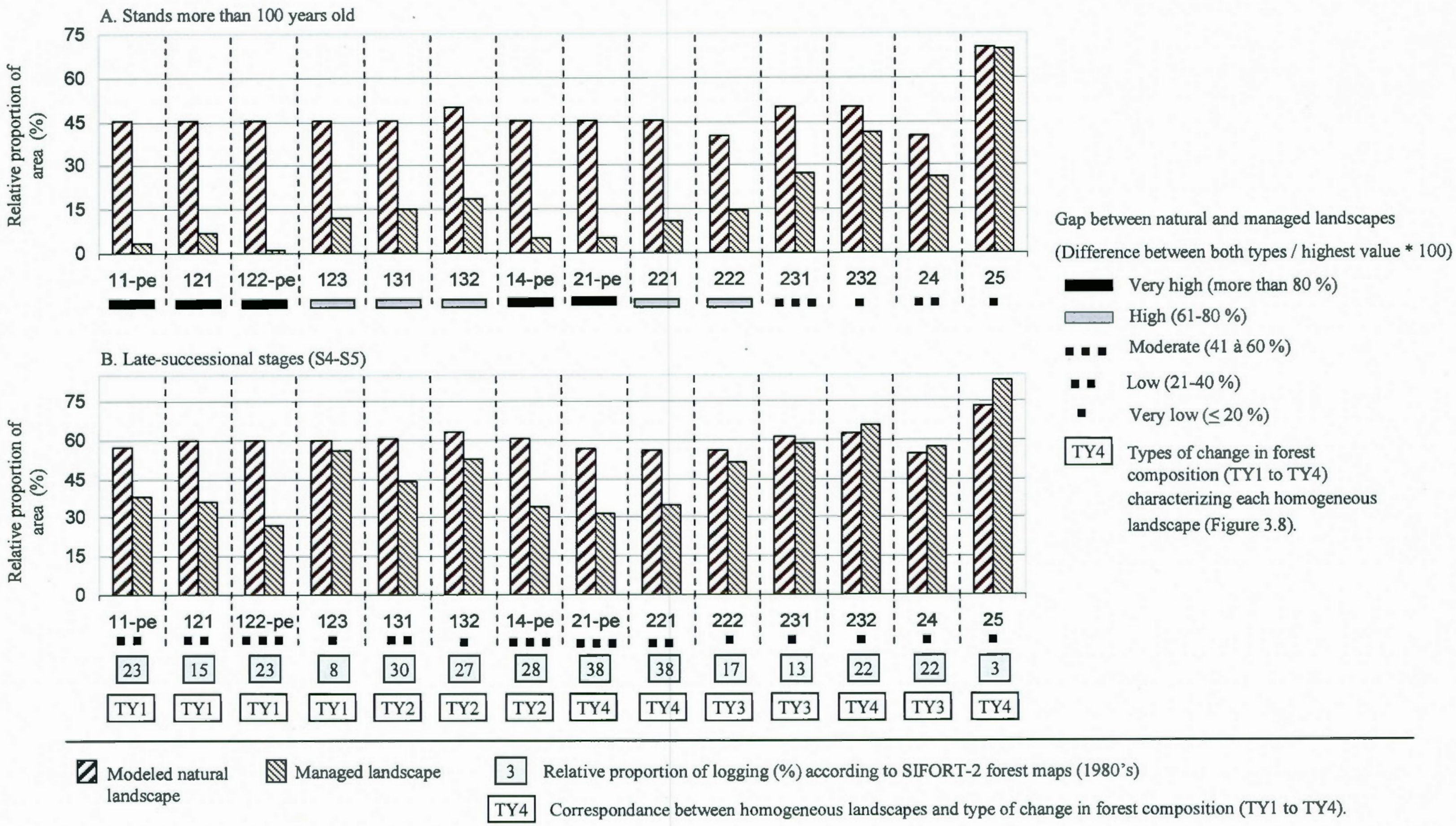
Appendix C1b. Modeled natural landscapes of the 14 homogeneous landscapes units characterizing the study area (Figure 3.2). The landscapes are described according to four types of forest composition (TY1-TY4, Figures 3.7, 3.8) and combinations of potential vegetation and successional stages represented by colors (Figure 3.8). Each combination is characterized by a temporal natural variability estimated on the basis of three fire cycles (C1, C2, C3) (Figures 3.4, 3.5)



Appendix C2. Comparison of homogeneous landscape units (e.g. HL : 121) representative of the four types of forest composition (TY1 to TY4) with respect to their natural and managed landscape. The natural composition is defined using fire cycle (Figure 3.5, Appendix A1) and forest dynamics (Figure 3.6). The managed landscapes have been defined from forest maps (1990-2000, third MRN 10-year inventory program). Forest composition is described according to potential vegetation types and successional stages (Figure 3.6). The managed landscape are first defined by considering logging (black bar) and second by logging distributed on a pro rata of conifer abundance in successional stages



Appendix C3. Comparison of natural and managed landscapes regarding their age structure and their forest composition. The 14 homogeneous landscapes are considered (Figure 3.2)



CHAPITRE 4

LES LIMITES DE L'ÉTUDE

Pierre Grondin et Sylvie Gauthier

Cette étude repose sur des concepts (ex. la végétation potentielle), des sources d'information (ex. les placettes d'inventaire dendrométrique), des analyses (ex. analyses de groupement) et des résultats variés (ex. cycle de feu). L'ensemble de ces éléments permet de répondre aux buts et objectifs poursuivis, mais plusieurs concepts, méthodes et analyses utilisés ont une portée limitée, méritent justification ou pourraient être améliorés dans le contexte de nouvelles études.

4.1 La matrice des variables réponses (matrice Y)

En regard de la première matrice utilisée, celle de la végétation, deux points sont discutés.

4.1.1 La description de la végétation

Dans les deux premiers chapitres, les thèmes des espèces ainsi que celui combinant les végétations potentielles et les stades évolutifs ont été décrits sur la base de placettes d'inventaire dendrométrique. Or, ces placettes ont été réalisées entre 1970 et 2000 dans le but de répondre à des besoins relatifs à l'estimation de volume ligneux. Cette méthode favorisait une surestimation des peuplements conifériens, les plus prisés pour la récolte forestière. Nous n'avons cependant pas quantifié cette distorsion et nous estimons que les résultats en sont peu affectés. Une façon rapide de mesurer le biais aurait été de comparer des portraits forestiers provenant des placettes avec ceux issus des cartes écoforestières. Au chapitre 1, la description du thème des espèces montre possiblement une proportion de conifères supérieure à ce qu'elle est. Au chapitre 2, les trois thèmes de végétation sont soumis à une analyse de redondance, de sorte que l'effet « placette » est en quelque sorte amoindri par les autres thèmes. Enfin, au chapitre 3, notamment au niveau de la modélisation de la dynamique forestière, la proportion de peuplements de fin de succession est considérée comme légèrement surestimée. Alors la proportion de feuillus de lumière est moindre qu'en réalité et l'importance de l'enfeuillement est légèrement sous-estimée.

4.1.2 Les végétations potentielles

Dans le contexte du troisième thème de végétation considéré dans cette étude, nous avons associé à chacune des placettes des inventaires dendrométrique et écologique une végétation potentielle. Normalement, l'identification d'une végétation potentielle découle de l'analyse du couvert forestier, de la végétation de sous-bois et d'un ensemble de variables ayant trait au milieu physique (e.g. le drainage) et aux perturbations naturelles et humaines (Blouin et Berger 2005). Dans le cadre de la présente étude, ces données n'étaient disponibles que pour les placettes de l'inventaire écologique, mais pas pour celles de l'inventaire dendrométrique. Dans le cas de ces dernières, la végétation potentielle a été identifiée essentiellement sur la base des essences forestières (voir chapitre 1). Les critères alors retenus s'inspirent des clés présentées dans les guides de reconnaissance des types forestiers produits par le MRN. Les végétations potentielles considérées dans cette étude sont également similaires à celles présentées par Harvey et al. (2002) et c'est pour cette raison que nous n'avons pas poussé notre analyse plus avant. L'une des suites de cette étude pourrait donc avoir comme objectif de caractériser les végétations potentielles par le biais de l'écologie numérique. Cette mise au point sur les végétations potentielles pourrait d'ailleurs être mise en lien avec les développements conceptuels récents des bassins d'attraction (Fletcher et al. 2014).

Dans un autre ordre d'idée, on peut s'interroger sur la pertinence d'avoir utilisé la notion de la végétation potentielle dans cette étude. Cet aspect est abordé à quelques endroits dans le texte, notamment dans l'article 1 où l'on justifie l'emploi de trois thèmes pour définir la végétation, soit les espèces, les types forestiers et la combinaison végétation potentielle-stade évolutif. L'utilisation de cette combinaison permet d'avoir une description portant sur la dynamique de la végétation. Quelques auteurs considèrent comme inadéquate l'utilisation du concept de la végétation potentielle (Chiarucci et al. 2010). Quatre principaux problèmes sont alors énoncés.

1- Le premier problème est que la plupart des données phytosociologiques proviennent d'échantillons positionnés subjectivement et qui ne permettent pas de généralisation sur les unités de végétation reproductibles.
2- Le deuxième problème est le choix de l'échelle spatiale dans laquelle la végétation potentielle est définie (niveau local) par rapport à celle dans laquelle elle est exprimée (niveau régional). Les unités de végétation sont généralement définies en utilisant un petit grain, telles que les données provenant de parcelles, alors que les résultats sont extrapolés à de vastes régions. Les généralisations que l'on fait à partir d'un faible nombre d'échantillons peuvent être considérées comme fragiles.
3- Le troisième problème est que dans bien des régions, les témoins non perturbés par l'homme sont rares de sorte qu'il est difficile de bien définir le stade de fin de succession de chacune des végétations potentielles caractérisant un territoire.
4- Enfin, le quatrième problème est que ce concept assume beaucoup de stabilité et de permanence. On insiste sur le fait que la végétation potentielle est une entité permanente de végétation, malgré les aléas des perturbations naturelles (superficie

et sévérité). Au final, le concept de bassin d'attraction semble mieux adapté aux processus de dynamique écologique en cours.

Cependant, dans notre territoire d'étude, les placettes ont été localisées au hasard et elles sont relativement nombreuses, ce qui fait en sorte que les résultats obtenus peuvent être appliqués à l'ensemble du territoire. De plus, la portion nord du territoire est relativement naturelle alors que la portion sud n'est que modérément affectée par les activités anthropiques. Dans ce dernier secteur, les proportions de stades évolutifs ne sont plus les mêmes que dans les paysages naturels et les peuplements de début de succession abondent. Dans ces cas, l'identification d'une végétation potentielle même dans les sites perturbés demeure possible. De plus, les sites permettant l'observation et la description de la végétation de fin de succession sont encore relativement nombreux. Enfin, bien que la notion de végétation potentielle s'applique relativement bien à notre territoire d'étude, on pourrait bonifier la définition du concept en lui assignant une possibilité de non-permanence. Par exemple, des sites propices à la végétation potentielle de la sapinière à bouleau blanc (MS2) pourraient, sous l'efffet des feux, se modifier en sites appartenant à la végétation potentielle de la sapinière à épinette noire (RS2). Cela se traduirait notamment par une augmentation de l'épinette noire et des éricacées. De tels transferts devraient se vérifier à l'aide d'études portant sur la dynamique forestière contemporaine et plurimillénaire. Enfin, il ne faut pas oublier que la justification première de l'utilisation du concept de la végétation potentielle dans cette étude était de mettre l'accent sur l'aspect dynamique de la végétation.

4.2 La matrice des variables explicatives (matrice X)

En ce qui concerne cette seconde matrice, quelques limites doivent être présentées.

4.2.1- La période d'origine des placettes d'inventaire dendrométrique

Les placettes d'inventaire dendrométrique ont également été utilisées afin de définir les variables explicatives portant sur la période d'origine de chacune des placettes. Ces périodes ont été utilisées dans tous les chapitres. Or, un premier biais vient du fait que lors des premiers inventaires (décennie 1970), un âge maximal de 120 ans était attribué aux espèces forestières, même si ces dernières étaient plus âgées. Compte-tenu que l'an 1990 a été considéré comme notre unité de référence afin d'homogénéiser les âges de tous les inventaires (année du début du troisième programme d'inventaire décennal), de nombreuses tiges sont issues de feux survenus en 1870. Pour cette raison, toutes les tiges dont l'année d'origine est inférieure ou égale à 1870 ont été classées avec la période 1851 (< 1870). La littérature (Bergeron et al. 2001, 2004) montre que les feux de la période 1851 proviennent surtout de feux survenus vers 1820.

Chacune des placettes a également été caractérisée en regard de son type d'origine, c'est-à-dire les feux ou les épidémies d'insectes. Cette classification reposait essentiellement sur la composition forestière. Ainsi, les peuplements dominés par le sapin (MS2-S4, S5) se sont vu assigner une origine d'épidémies d'insectes correspondant aux périodes proposées par Morin 1994 : vers 1870 ou vers 1920. La majorité des peuplements affectés par l'épidémie de la période 1950 ont été classés avec l'une des épidémies précédentes sur la base des grosses épinettes dominantes et relativement âgées. En fin de compte, la classification des placettes d'inventaire par période et par type d'origine a nécessairement influencé les résultats d'au moins deux façons. La première est qu'elle a favorisé le partitionnement du territoire en trois sections longitudinales : le sud (épidémies de TBE), le centre (feux de la période 1921) et le nord (feux de la période 1851). Ce partitionnement structure l'ensemble de l'étude, depuis les gradients écologiques (chapitre 1) jusqu'au façonnement des unités homogènes (chapitre 2). Le second impact de la classification des placettes est la forte variation expliquée par seulement les perturbations naturelles (PNu). Tel qu'expliqué dans les annexes du chapitre 1, chacune des trois bandes décrites précédemment domine le territoire alors que des changements de climat et de milieu physique se réalisent. Cet anachronisme crée une forte variation unique dans la famille des perturbations naturelles. Grondin et al. (2007), dans leurs analyses du partitionnement de la variation de la végétation réalisées sur l'ensemble du Québec méridional, n'ont pas classé les placettes d'inventaire dendrométrique selon leur origine. Chez ces auteurs, la variation unique expliquée par les diverses familles est négligeable. De nombreuses placettes d'inventaire dendrométrique ont également été réalisées dans les portions de territoire fortement affectées par les activités anthropiques (feux, coupe). Ces placettes ont été attribuées à la période 1951 et elles forment une variable classée avec la famille des perturbations humaines. Cette variable, que nous avons décrite avec plus de détails dans les annexes du chapitre 3, joue un rôle important dans l'importance accordée à cette famille de variables explicatives.

4.2.2 Le climat

Les variables climatiques ont été générées par le logiciel BioSim à partir de 37 stations inégalement réparties sur le territoire (Chapitre 1, annexe 2). Les stations sont principalement localisées dans les portions les plus fortement urbanisées, notamment les régions du lac Saint-Jean et de l'Abitibi. La portion nord-ouest du territoire nous semble la plus négligée et cette dernière peut être notamment caractérisée par la station de Waskaganish localisée au nord du territoire d'étude. Il nous est difficile de juger de la qualité des données climatiques estimées par BioSim. La question qui demeure en suspens est donc : est-ce que le climat serait une variable dominante, ou du moins plus importante que les perturbations naturelles, si les valeurs avaient été de meilleure qualité? Nous sommes enclins à croire que non, en nous appuyant sur le partitionnement réalisé à l'échelle du Québec par Grondin et al. (2007), partitionnement dominé par le climat dans les traitements réalisés à l'échelle du Québec méridional. Nous supposons donc que l'effet mineur du climat indique que le gradient étudié ici n'est pas assez étendu pour y voir un effet dominant.

4.3 Les analyses

Les analyses numériques ont été réalisées simultanément sur les trois thèmes de végétation : les espèces forestières, les types forestiers et la combinaison des végétations potentielles et des stades évolutifs. Après de multiples analyses réalisées sur les thèmes pris individuellement et leurs combinaisons, nous avons choisi de travailler sur trois thèmes parce qu'ils nous permettent de prendre en compte l'ensemble de l'hétérogénéité de la végétation. L'ensemble des gradients : latitudinal, latitudinal-oblique, longitudinal, sont considérés lorsque les analyses sont réalisées avec les trois thèmes. Si l'on n'avait pas pris en compte le thème des types forestiers, une partie du gradient latitudinal oblique aurait été oubliée. On devrait également voir l'association des trois thèmes comme une richesse dans le sens qu'il s'agit de trois façons complémentaires d'aborder l'hétérogénéité de la végétation. Le thème des espèces laisse libre recours aux caractéristiques intrinsèques de chacune d'elles en regard de son mode de reproduction et de croissance (Hubbell 2001). Le thème des peuplements forestiers est étroitement lié à celui de la niche écologique. Enfin, les végétations potentielles et les stades évolutifs intègrent la dynamique forestière. Les trois thèmes permettent ainsi de démontrer que l'intégration des familles de variables explicatives caractérise autant le thème associé au concept de neutralité (Hubbell 2001) que les thèmes liés à la niche écologique (Hutchinson 1957). En fin d'analyses, on a compris le comportement des trois thèmes de végétation et tous ont contribué à expliquer une portion de la variation.

4.3.1 L'analyse de redondance (RDA)

Les trois thèmes de végétation (matrice Y) et les quatre familles de variables explicatives (matrice X) formant la base de cette étude (chapitres 1 et 2) ont été traités au moyen d'une analyse de redondance (RDA). Cette analyse a été utilisée parce qu'elle permet de définir les liens entre la végétation et ses variables explicatives au moyen de relations linéraires (Dray et al. 2012). La RDA peut être considérée comme une extension de la régression multiple. Elle repose sur des relations linéaires établies entre l'ensemble des variables explicatives et chacune des variables-réponses. Or, considérant le grand nombre de variables à l'étude, il se pourrait que certaines relations ne soient pas linéaires (Økland 1999, Austin 2002, Wagner 2004). Vérifier la linéarité des relations entre les variables explicatives et les variables réponses représente un travail énorme. Pour résoudre ce problème, Makarenkov et Legendre (2002) ont développé une méthode dénommée : la RDA polynomiale. Plus spécifiquement, des polynomes sont créés au niveau des variables explicatives. La RDA polynomiale permet d'obtenir une augmentation notable de la quantité de variation de Y expliquée par le modèle. Malheureusement, cette méthode s'est avérée complexe d'utilisation, au point que Legendre et Legendre (2012) n'en font pas état. Comme solution de rechange, il est proposé de réaliser une sélection des variables explicatives (forward selection) et de n'utiliser que les variables les plus significatives dans la RDA (Daniel Borcard, communication personnelle). Cette avenue, que nous n'avons pas empruntée, serait un moyen de pousser plus loin notre étude. Par contre, il est important de préciser que les variables explicatives les plus importantes dans la répartition de la végétation montrent une relation de linéarité le long des gradients environnementaux. Ces variables sont principalement le nombre de jours de croissance (GDD), la proportion de peuplements affectés par les épidémies légères de la tordeuse des bourgeons de l'épinette (Sbom), la proportion de peuplements ayant comme origine les feux de la période 1921 (1921f), la proportion de peuplements issus des feux de la période 1851 (1851f) et la différence d'élévation entre les portions les plus basses et les portions les plus hautes des districts écologiques (Ele) (Chapitre 2, annexe 5).

Par ailleurs, on sait qu'en régression linéaire, une attention particulière est accordée à l'analyse des résidus et de l'autocorrélation. Ces analyses ont essentiellement comme but d'étudier la matrice des résidus dans le but de voir si certaines structures spatiales n'auraient pas été oubliées ou négligées. Ces analyses seraient surtout intéressantes à des échelles plus fines que celle à laquelle nous avons travaillé (Daniel Borcard, communication orale). Sur notre territoire d'étude, il serait surprenant que les résidus apportent de nouvelles connaissances, de sorte que nous nous sommes concentrés sur les ordinations provenant de la matrice des valeurs estimées. En effet, toujours dans un contexte de comparaison entre les régressions et les analyses multivariées, on peut souligner le fait que la matrice des résidus associée aux régressions ne comporte pas de valeurs négatives. Ce n'est cependant pas le cas dans les analyses multivariées parce que, par définition, dans le processus de réalisation de la RDA, les valeurs sont d'abord centrées avant d'être soumises aux régressions de l'ensemble des variables explicatives sur chacune des variables réponses. Cette procédure entraîne nécessairement des matrices de résidus avec valeurs négatives. Théoriquement, ces valeurs ne font pas de sens en écologie (un recouvrement d'espèces ne pouvant être négatif). Par contre, et considérant que la matrice des résidus fait l'objet d'une analyse en composantes principales dont la finalité est une ordination, la présence de valeurs négatives dans la matrice des résidus ne pose aucun problème. Le but ultime est de comparer les variables sur des ordinations, et la présence de valeurs négatives ne nuit aucunement à cette comparaison.

À la lumière de ces considérations, on peut se demander si nous aurions pu orienter différemment cette étude qui se situe dans la lignée des enseignements gravitant autour de Legendre et Legendre (2012) ainsi que de Dray et al. (2012) et qui ouvre la porte aux analyses sur le partitionnement de la variation de la végétation. Certains travaux australiens (Austin 2002) et scandinaves (T. Okland 1996, R. Okland 1999) se sont plutôt avérés complémentaires à notre démarche. Si de nouvelles pistes étaient à explorer, nous aurions possiblement intérêt à cheminer vers des modélisations actuelles et futures des espèces, en lien avec les variables du milieu physique et le climat (Ohmann et al. 2011, Halvorsen 2012).

4.3.2 Le regroupement des variables-réponses et des variables explicatives

Tel que précisé précédemment, l'un des buts de la RDA est de positionner les variables-réponses ainsi que les variables explicatives sur des ordinations formées par les axes canoniques expliquant le mieux les variations du système écologique à l'étude. Ces ordinations présentent l'ensemble des variables (près de 80), ce qui nuit à une vue-synthèse. On a donc rassemblé les variables à l'aide de groupements réalisés sur l'ensemble des axes canoniques. Cette façon de procéder a été examinée relativement au nombre d'axes canoniques utilisé pour réaliser les groupements. Une première solution aurait été de considérer seulement les premiers axes, notamment les trois premiers qui comptent pour plus de 50 % de la variabilité, sous prétexte que les autres axes étaient inutiles en raison de leur faible pouvoir explicatif. Cette option n'a pas été retenue et nous avons opté pour la prise en compte de l'ensemble des axes, donc de l'ensemble de la variabilité.

4.3.3 Le partitionnement de la variation de la végétation (RDA partielles)

Un défi fondamental en écologie est de comprendre le rôle des variables environnementales (les déterminants) dans le façonnement de l'hétérogénéité de la végétation. Traditionnellement, les écologistes se sont appuyés sur le concept des niches environnementales pour expliquer la variabilité des communautés dans les paysages (Hutchinson 1957) : chacune des communautés avait sa niche écologique, c'est-à-dire son milieu de croissance. Par la suite, et comme nous l'avons déjà précisé dans l'introduction, le cheminement conceptuel a dévié vers une logique appuyant l'importance des perturbations naturelles comme principal vecteur expliquant l'hétérogénéité des paysages. Dans un troisième temps, et c'est le paradigme qui a été considéré prioritaire dans cette étude, l'intérêt a porté sur l'intégration de plusieurs familles de variables explicatives. L'intégration n'est pas un phénomène nouveau (Daubenmire 1936), mais sa démonstration mathématique a subi un cheminement graduel au cours des dernières années vers la définition du partitionnement de la variation de la végétation (Borcard et al. 1992, Økland 1996, Økland 1999, Økland and Eilertsen 1994, Legendre et Legendre 2012, Halvorsen 2012). Ces divers auteurs ont notamment précisé que la variation inexpliquée était associée aux variables environnementales non mesurées, à la stochasticité des processus biologiques, tels la dispersion, l'établissement et la mortalité, et au manque d'ajustements entre les données et les variables réponses (*the lack-of-fit of data to the response model*). Enfin, Gilbert et Bennett (2010) ont démontré une certaine instabilité des résultats du partitionnement selon la densité d'échantillonnage. En raison de la multitude de sources d'information utilisées dans cette étude et la densité d'échantillonnage, nous estimons que cette instabilité est absente de nos résultats.

La RDA et les diagrammes d'ordination qui en résultent sont utilisés notamment pour visualiser et comprendre le chevauchement entre les variables-réponses et les variables. Nous avons accordé beaucoup d'importance à l'établissement de ces relations, sans quoi les résultats du partitionnement de la variation de la végétation ne pourraient être expliqués sur une base écologique.

Le partitionnement de la variation de la végétation vient quantifier le chevauchement observé entre les variables-réponses et les variables explicatives. Rares sont les études qui ont considéré, comme c'est notre cas, quatre familles de variables explicatives. Rares sont également les études qui ont pris en compte autant les variables explicatives naturelles (climat, milieu physique, perturbations naturelles) que les variables anthropiques (perturbations humaines). Par ailleurs, la majorité des études portant sur le partitionnement de la variation de la végétation (*variation partitioning*) favorise une intégration de plusieurs familles de variables explicatives dans l'explication de la variation de la végétation. Tout compte fait, il existe des liens entre le paradigme de l'hétérogénéité et le partitionnement multiple de la variation de la végétation. Autant la décennie 1970 a vu l'apparition de travaux sur l'importance des feux (Heinselman 1973; Rowe et Scotter 1973), autant la décennie 1990 a permis de quantifier les relations entre les familles de variables explicatives. En définitive, les deux aspects ont joué un rôle majeur dans la compréhension du paradigme de l'hétérogénéité. En d'autres termes, la prise en compte 1) des perturbations naturelles et humaines ainsi que 2) la démonstration de l'intégration des variables explicatives sont deux prérequis au paradigme de l'hétérogénéité. La présente étude joue un rôle-clé dans le second élément.

Enfin, il faut être prudent sur la façon dont les diagrammes d'ordination et les résultats du partitionnement peuvent être interprétés relativement à l'importance des familles de variables explicatives. Une erreur consisterait à interpréter divers résultats partiels portant sur l'importance des variables par rapport au résultat d'ensemble du partitionnement. Par exemple, la figure 3 du chapitre 1 (ordination des variables explicatives) ainsi que la figure 5A du chapitre 2 pourraient être comprises comme favorisant le climat dans l'explication de l'hétérogénéité des paysages. Cette avenue s'avèrerait erronée. Il faut plutôt se référer aux résultats globaux formant la figure 5 du chapitre 1. Cette figure montre que le climat doit être considéré comme une famille sous-dominante.

4.4 La cartographie des écosystèmes

La production de cartes de végétation et de cartes de variables explicatives a occupé une place importante dans cette étude. Dans le chapitre 1, des cartes thématiques ont été dressées dans le but de décrire le chevauchement entre les variables-réponses et les variables explicatives (Appendices 3A, 3B et 3C). Ces cartes reposent sur des groupements K-means réalisés sur les données brutes. Dans le chapitre 2, deux types de cartes ont été produites.

- Le premier type vise la comparaison des systèmes de classification provenant de sources multiples : la végétation (Figure 2.3), les familles explicatives naturelles (Appendice 3A), la végétation – le milieu physique – et le climat (Appendice 3B) et la végétation – les perturbations naturelles et le climat (Appendice 3C). Ces cartes proviennent soit de groupements K-means réalisés sur les données brutes ou sur l'ensemble des axes canoniques issus d'analyses de redondance (RDA).
- Le second type vise l'élaboration d'un système hiérarchique de classification écologique (Figures 2.4 à 2.7). Le système est en lien étroit avec les axes canoniques de la RDA (Figure 2.4).

Le problème soulevé par notre approche est la proximité entre les méthodes proposées pour les chapitres 1 et 2. Les deux chapitres reposent sur la même analyse de redondance (RDA), ce qui pourrait être considéré comme une limite possible de l'étude. Par ailleurs, dans le chapitre 1, les résultats de la RDA sont essentiellement utilisés à des fins d'ordination et de description du chevauchement entre les variables-réponses et les variables explicatives. Tous ces éléments sont préparatoires à l'interprétation des résultats du partitionnement. Dans le chapitre 2, les résultats sont à la base de la formation d'unités homogènes. Nous considérons que les buts spécifiques de chacun des chapitres et d'une utilisation distincte d'une même RDA justifient la présence de deux chapitres.

Plus spécifiquement, de légers problèmes ont été rencontrés lors de l'élaboration de cartes dont les subdivisions reposent sur le logiciel *K-means*. Ces problèmes proviennent surtout du fait que les groupements présentés ne sont pas nécessairement hiérarchiques d'un niveau à l'autre. Cela oblige à tirer une interprétation des résultats moins rigoureuse lors de l'élaboration d'un système hiérarchique de classification. Ces divers éléments sont notamment discutés dans l'appendice 4 du chapitre 2.

De plus, certaines avenues pourraient être explorées, notamment celles ayant trait au *fuzzy clustering* (De Cáceres et al. 2010; Borcard et al. 2011; Duff et al. 2013). Les méthodes *Fuzzy* ont été développées afin de représenter l'incertitude dans la délimitation des classes de végétation ou des écosystèmes. Ces méthodes pourraient montrer que certains districts écologiques sont intermédiaires entre deux unités géographiques. Dans les analyses de groupement traditionnelles, les données sont subdivisées en groupes distincts. Dans la méthode *fuzzy*, les éléments de classification (districts écologiques) peuvent appartenir à plus d'un groupement, et être associés à chacun des groupes selon un niveau d'adhésion. Chacun des niveaux indique la force de l'association entre cet élément de classification et un groupe particulier.

Une autre façon de bonifier la cartographie des unités homogènes serait d'utiliser les arbres de régression multiples (*mean regression tree* -MRT). Il s'agit d'une méthode de partitionnement divisive avec contrainte impliquant deux matrices, l'une de variables-réponses et l'autre de variables explicatives. Le résultat est un arbre dont les groupes terminaux sont composés de sous-ensembles de sites choisis pour réduire au minimum la somme des carrés intra-groupe (comme dans un regroupement K-means), mais où chaque partition successive est définie par un seuil correspondant à un état de l'une des variables explicatives. Parmi les nombreuses solutions possibles de subdivisions, la variable retenue est celle qui a le meilleur pouvoir prédictif (Borcard et al. 2011). Enfin, nous n'avons pas comparé dans le cadre de cette étude les unités homogènes (Chapitre 2) avec les régions écologiques du MRN (Saucier et al. 2009). Les deux systèmes ont comme données de base les districts écologiques (Figure 1). Par contre, dans le contexte des unités homogènes, les districts écologiques sont, tout d'abord, caractérisés en fonction de leur milieu physique, de leur climat et de leurs perturbations (naturelles et humaines). Par la suite, des analyses numériques mènent à une hiérarchie d'unités homogènes. À l'opposé, lors de la formation des régions écologiques, les districts écologiques sont essentiellement caractérisés par leur milieu physique et la végétation (végétations potentielles – stades évolutifs). Les districts écologiques sont ensuite regroupés manuellement pour définir des paysages régionaux, des régions écologiques et des domaines bioclimatiques. Les perturbations naturelles sont peu considérées et ces dernières viennent caractériser les entités écologiques, *à postériori* (Gauthier 2001). Tout considéré, nous croyons que les unités homogènes sont plus près des processus qui gèrent la répartition des écosystèmes boréaux (Rowe 1980, Rowe et Sheard 1981, Bailey 2009). Par ailleurs, l'ensemble de la démarche liant 1) les gradients écologiques (chapitre 1, 2), le partitionnement de la variation de la végétation (chapitre 1 et 3) et la cartographie des unités homogènes (chapitre 2) favorise une meilleure compréhension des résultats.

Il nous est difficile de statuer sur la pérennité plurimillénaire des unités homogènes que nous avons développées. Il est possible que certaines d'entre elles ne soient que le fruit de perturbations passées ou même récentes à l'intérieur de grands ensembles écologiques similaires. À priori, nous estimons que la majorité des unités sont relativement permanentes, à l'exception de celles localisées dans la plaine argileuse de l'Abitibi qui se sont individualisées sous l'influence des activités anthropiques (annexes du chapitre 2). Les travaux de Boulanger et al. (2013) sur les changements futurs causés par les feux montrent que même si le régime des feux change (fréquence, intensité), les limites des unités à la base de l'étude ne seront pas modifiées. Dans un autre ordre d'idée, on pourrait se demander si les unités homogènes sont suffisamment grandes pour réaliser une analyse d'écarts (chapitre 3). Les unités ont une superficie moyenne de 10 500 km^2, ce qui est très vaste. Cette superficie excède les superficies considérées par Turner et al. (1993) dans leur classification de territoires sur la base des feux et de la dynamique forestière. De plus, la superficie moyenne des unités homogènes excède la superficie moyenne des feux qui est de l'ordre de 2 000 km^2 (Appendice A2c).

Le système du MRN regroupe des districts écologiques pour d'abord former des unités de paysages régionaux (Robitaille et Saucier 1998), puis des régions écologiques et autres niveaux supérieurs du système de classification écologique (Saucier et al. 2009). Dans le contexte des unités homogènes, le niveau équivalent à celui des paysages régionaux est atteint lorsque chacune des unités homogènes est soumise à des traitements similaires à ceux de l'ensemble du territoire. Plus spécifiquement, à la figure 1, les districts écologiques de l'unité 232 ont été soumis à une analyse de redondance (RDA) et le produit obtenu est apparenté à celui des unités de paysages.

Bien des systèmes de classification reposent essentiellement sur la répartition de la végétation avec, en soutien, des descripteurs du climat et du milieu physique. Appuyer les systèmes de classification sur les variables permanentes du milieu a longtemps été considéré comme garant de la pérennité des délimitations (Jurdant et al. 1977). Le système des unités homogènes va plus loin en faisant appel à l'idée de liens étroits entre la végétation, le milieu physique et les perturbations naturelles. Les résultats du partitionnement démontrent l'existence de ces liens et ils nous permettent d'affirmer qu'un système reposant sur la végétation, le climat, le milieu physique et les perturbations naturelles est aussi permanent que celui axé essentiellement sur le milieu physique. L'argumentaire selon lequel les perturbations sont aléatoires (imprévisibles) et qu'elles ne devraient pas être considérées dans l'élaboration des systèmes de référence ne tient donc pas la route. Cependant, les régimes peuvent changer, ainsi que leurs interactions (ex. feux et épidémies d'insectes). Cela ne devrait cependant pas influencer les limites.

Par contre, la prise en compte des activités anthropiques pourrait être vue comme un obstacle à l'élaboration d'un système de référence. Doit-on alors les ignorer ou plutôt les étudier afin de mieux comprendre leur impact? Cette deuxième solution a été privilégiée. Dans l'ensemble de cette étude, les connaissances sur les perturbations humaines ont suivi la progression suivante :

Chapitre 1- reconnaissance des activités humaines par l'entremise du partitionnement de la variation de la végétation.

Chapitre 2- délimitation d'unités homogènes (n=5) sur la base du quatrième axe canonique d'une analyse de redondance (RDA).

Chapitre 3- Comparaison des unités homogènes fortement affectées par les activités anthropiques avec les unités homogènes naturelles.

Nous concluons que les activités anthropiques ont été un obstacle constant tout au cours de cette étude. Il aurait été beaucoup plus facile de travailler dans un territoire totalement naturel. Par contre, cerner l'impact des perturbations humaines aura été un défi intéressant à relever. Le défi est d'autant plus grand que les variables descriptives des activités anthropiques sont difficiles à isoler. Par exemple, les feux d'origine humaine sont une sous-classe d'une variable décrite dans des documents d'archive. De plus, le lien entre les forêts provenant de la période 1951 et les activités anthropiques (portion sud du territoire) n'est détectable qu'après une analyse détaillée de l'information. L'étape suivante serait de caractériser plus finement l'impact des activités anthropiques, leur chronologie, leur incidence sur la dynamique forestière... par des relevés de terrain.

Figure 1. Comparaison entre le système du MFFP et le système des unités homogènes proposé dans la présente étude

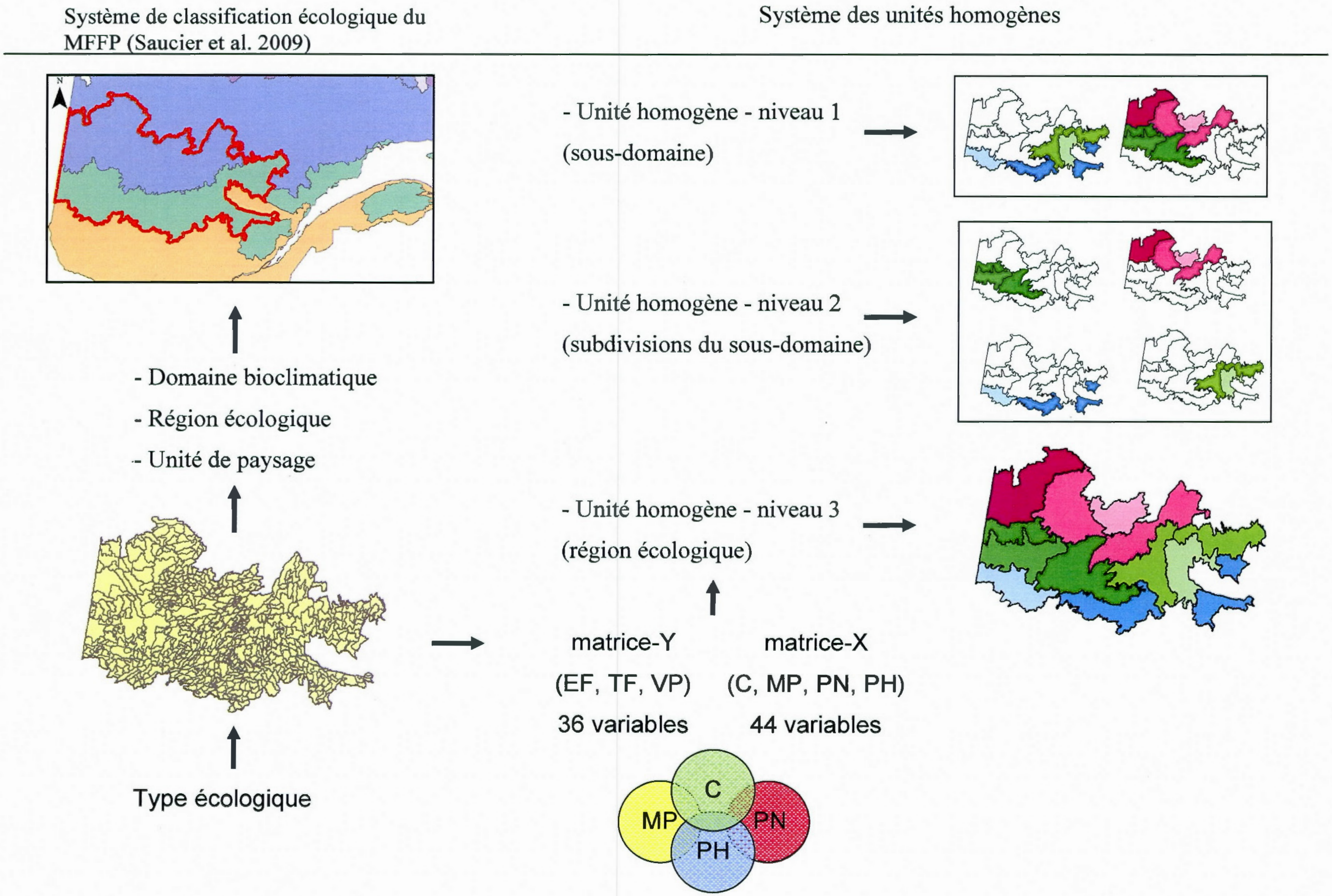
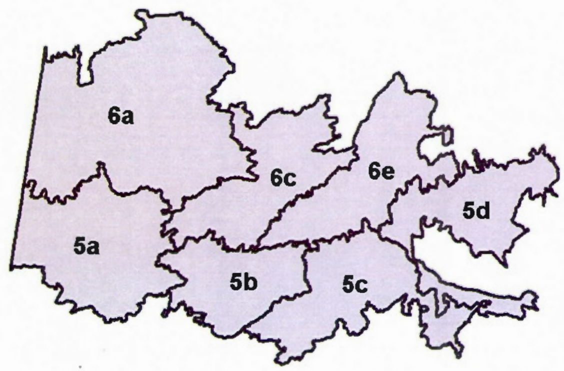


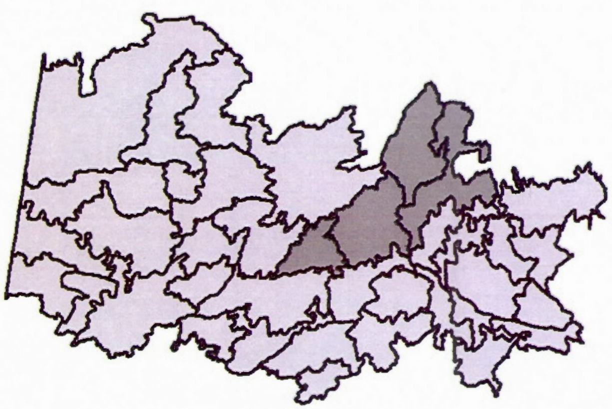
Figure 1. Comparaison entre le système du MFFP et le système des unités homogènes proposé dans la présente étude (suite)

Système de classification écologique du MFFP (Saucier et al. 2009)

Les régions écologiques (n =8)

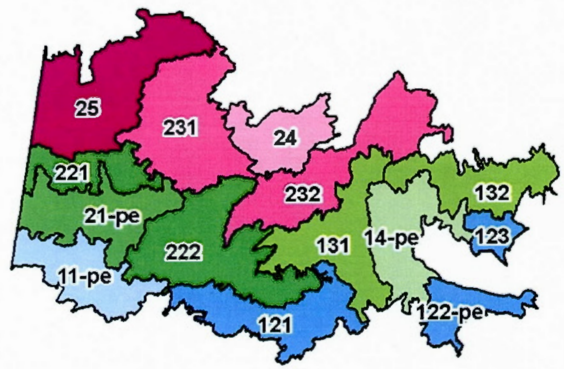


Les unités de paysage régional (n = 38)

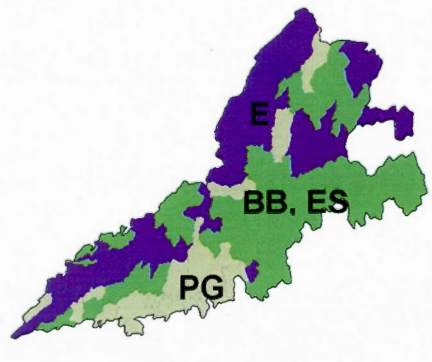


Système des unités homogènes

Les unités homogènes (niveau 3, n = 14)



Les unités homogènes (niveau 4, exemple de l'unité 232)
E : dominance de pessières noires
BB, ES : dominance de bétulaies blanches et de pessières noires à sapin
PG : dominance de pinèdes grises



4.5 Les cycles de feu

Le cycle de feu est l'un des éléments importants à considérer dans la détermination du paysage naturel (Figure 3.3). La méthode la plus typique de le définir est de réaliser une carte montrant l'année d'origine de chacun des peuplements d'un secteur d'étude et, à partir de là, estimer un âge moyen correspondant à un cycle de feu (Heinselman 1973; Bergeron et al. 2001, 2004). Sur le territoire qui nous préoccupe, plusieurs secteurs ont été étudiés dans le but de définir un cycle de feu. Ceux-ci couvrent partiellement 8 des 14 unités homogènes délimitées à la figure 3.4. Pour associer un cycle de feu à l'ensemble des unités homogènes, nous avons eu recours aux placettes d'inventaire forestier (Chapitre 1, Appendice 2). Ces dernières ont été utilisées afin de définir des proportions relatives de placettes en regard de différentes périodes d'origine (Chapitre 3, Appendice A9). Cette manœuvre est délicate puisqu'elle repose sur le plus vieil arbre-étude d'une placette et que ce dernier ne provient pas nécessairement des espèces qui se sont installées après un feu. De plus, l'approche par placette, qui s'appuie sur l'inventaire des peuplements matures (50 ans et plus), ne tient pas compte des feux récents. Une approche bonifiée consisterait donc à définir le cycle de feu en combinant les placettes ainsi que les superficies récemment incendiées. Les proportions relatives de placettes par différentes périodes ont également été utilisées afin de regrouper les unités homogènes selon trois cycles de feu. Les regroupements ont été faits visuellement et en considérant d'autres variables, comme la texture du sol. Au final, la méthode demeure déficiente, mais conséquente avec la qualité des données disponibles.

Cependant, afin de valider notre approche par placette et le regroupement des unités homogènes en cyles de feu, nous avons également analysé les données sous l'angle de la proportion de peuplements de plus de 100 ans selon les cartes forestières

(Chapitre 3, Appendice A10). Nous considérons ces deux approches comme complémentaires. Tout considéré, les cartes de feu réalisées demeurent perfectibles (Figure 3.4) mais nous les estimons suffisamment précises considérant le but recherché qui est la définition des paysages naturels. Une certaine confiance dans les résultats obtenus est également acquise lorsque nous comparons la carte des cycles de feux réalisée par Grondin et al. (2007), selon la même méthodologie que celle de la présente étude, avec la carte des cycles de feu récemment produite dans le cadre du tracé de la limite nordique (Ministère des Ressources naturelles 2013).

Enfin, étant donné que l'ensemble de notre démarche relative aux cycles de feu visait à compléter une information existante et portant sur des cartes d'origine (Figure 3.4), nous n'avons pas réalisé d'analyses supplémentaires. Ces analyses auraient comme premier objectif de vérifier si la distribution des classes d'âge adopte une exponentielle négative. De plus, à l'aide d'analyses de survie, il aurait été possible d'estimer un cycle de feu (Le Goff 2007). Une seconde raison pour laquelle ces analyses n'ont pas été effectuées est que nous considérons les informations de base (placettes d'inventaire) de qualité insuffisante pour être soumises à des analyses statistiques sophistiquées.

4.6 La structure d'âge de la forêt

La détermination de la structure d'âge d'un paysage est un sujet relativement complexe puisque la méthode utilisée doit prendre en considération l'ensemble des variables qui contribuent au développement de cette structure. Dans le contexte de la présente étude, la structure d'âge a été définie à l'aide des placettes d'inventaire dendrométrique pour lesquelles nous possédons un âge (n = 53 635). Notre hypothèse est que ces placettes reflètent les conditions dans lesquelles les forêts ont évolué, notamment en ce qui touche leurs perturbations naturelles (feux, chablis, épidémies d'insectes). Les placettes contenues dans chacune des unités homogènes ont été utilisées afin d'en élaborer la structure d'âge. Pour minimiser l'effet des lacunes liées à l'échantillonnage et au dénombrement des cernes, les âges des placettes ont été regroupés en périodes. Ces données ont ensuite été utilisées afin de définir un cycle de feu et ce dernier a servi à élaborer une distribution théorique des classes d'âge (van Wagner 1978).

Des études empiriques ont partiellement soutenu l'idée que la distribution théorique des classes d'âge adoptait la forme d'une exponentielle négative (Bergeron et al. 2001). Sous les régimes de perturbations typiques de la forêt boréale, Boychuk et Perera (1997) ont estimé que la structure d'âge de la forêt ne suivait pas une distribution exponentielle, même à de très grandes échelles spatiales, en raison de la distribution hétérogène des perturbations. Par exemple, les incendies dans notre zone d'étude ont eu lieu principalement autour de 1820 et de 1910 à 1920 (Bergeron et al. 2001); cette répartition peut être considérée comme une exponentielle négative lorsque les feux sont regroupés en périodes (par exemple 1851-1891-1921-1951). La distribution exponentielle est encore moins évidente dans les régions où les incendies sont peu fréquents et de grande taille (Bouchard et al. 2008). Armstrong (1999), par le biais d'estimations de taux de combustion moyens réalisées par des simulations de Monte Carlo démontre que la modélisation du régime des perturbations ne conduit pas à une distribution des classes d'âge à l'équilibre. Les auteurs suggèrent qu'un grand nombre de changements sont attribuables au hasard plutôt qu'à des changements climatiques ou anthropiques.

Dans la zone d'étude, nous estimons que l'utilisation de la distribution de probabilité de Van Wagner (1978) était la meilleure façon de définir une structure d'âge théorique. Cependant, nos structures d'âge ne considèrent pas directement l'effet des épidémies d'insectes en termes de types de composition de la forêt et de la classe d'âge (Boucher et al. 2011). Notre approche est justifiée par la variabilité relativement élevée et le faible impact des infestations d'insectes sur la composition de la forêt et de la structure d'âge dans la zone d'étude (Bouchard et al. 2007). La situation qui prévaut dans les écosystèmes boréaux diffère de celle de la zone tempérée, où l'impact des épidémies est plus fort (Bouchard et al. 2007, Duchesne et Ouimet 2008). En outre, les placettes d'inventaire forestier et les cartes utilisées dans cette étude sont elles-mêmes un reflet des épidémies antérieures. L'impact des épidémies d'insectes est donc considéré de manière indirecte dans notre étude.

Malgré ces limites, peu de suggestions ou d'approches pratiques ont été proposées. Toutefois, l'article d'origine de van Wagner (1978) permet d'entrevoir une piste de solution pour résoudre le problème. En effet, van Wagner, en l'absence de toute autre information, suppose que la probabilité de feu annuelle est constante dans le temps, ce qui est confirmé par son équation exponentielle. Il serait possible à ce stade d'introduire une probabilité de feu annuelle, ou à l'échelle de la décennie, probabilité qui serait fonction des diverses variables environnementales (climat, composition du paysage, etc.) et de l'historique des feux. Une telle approche préserverait la logique du modèle de probabilité géométrique sous-tendant la composition du paysage issu de feux. L'évaluation de cette probabilité représente un défi intéressant à relever. Une meilleure évaluation du cycle de feu aurait nécessairement des répercussions sur la structure d'âge des paysages. On y observerait une plus grande variabilité. Par contre, le fait que nous ayons considéré de grandes classes d'âge dans la description des structures d'âge atténue cette lacune. En bout de piste, la principale variable qui découle de l'analyse du cycle de feu et de la structure d'âge est la proportion de forêts de plus de 100 ans. Cette dernière valeur est obtenue avec une précision acceptable, peu importe la méthode retenue en ce qui a trait aux probabilités de feu.

4.7 La dynamique forestière

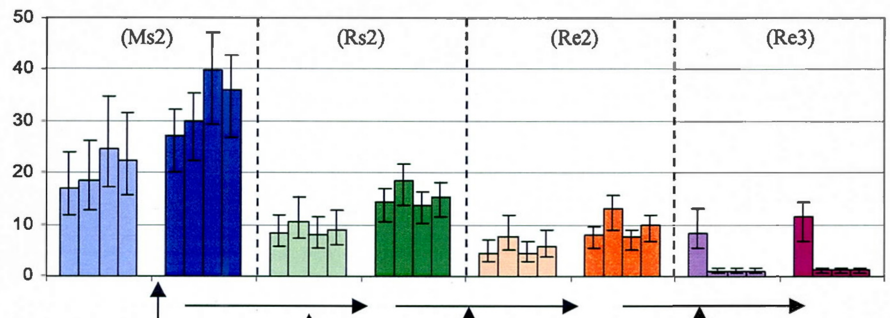
La modélisation de la dynamique forestière est le second élément à prendre en compte dans la détermination du paysage naturel (Figure 3.3). L'objectif de cette modélisation est de définir des proportions de peuplements selon leur stade évolutif (début, milieu et fin de succession) et leur classe d'âge. On s'intéresse donc aux grands changements de végétation qui se réalisent à l'échelle du paysage. Dans le cadre de cette étude, la description de la dynamique repose sur la notion de la végétation potentielle. Les placettes de l'inventaire dendrométrique sont à la base de la modélisation de la dynamique. Les placettes sont classées selon leur stade évolutif (S2-S3-S4-S5) et leur âge (à l'appui du plus vieil arbre-étude). Par la suite, ces données sont soumises au modèle de Weibull. La première limite de cette méthode repose sur la classification de certains peuplements forestiers en regard de leur stade évolutif. Par exemple, les pessières peuvent être considérées autant comme des peuplements de début de succession (on peut les observer immédiatement après feu) que des peuplements de fin de succession. Dans de tels cas, la classe d'âge a été utilisée afin de départager les divers groupes. Par exemple, dans le cas des pessières, les peuplements de 90 ans et moins ont été considérés comme en début de succession. La seconde limite de cette méthode est qu'elle repose sur l'hypothèse que les placettes soient représentatives de la superficie occupée par les divers stades évolutifs et de leur âge. On sait qu'il y a un biais favorisant les peuplements conifériens dans le choix des placettes, de sorte que ces peuplements sont possiblement surestimés comparativement aux peuplements feuillus (début de succession). Enfin, la troisième limite est que tous les peuplements évoluent selon une séquence de peuplements qui est une représentation trop simplifiée de la réalité. Plus spécifiquement, et par exemple, le peuplement feuillu évolue vers le peuplement mélangé puis vers le peuplement coniférien. Dans la réalité, la dynamique est beaucoup plus complexe et des peuplements de composition variée (feuillu, mélangé, coniférien) peuvent se développer immédiatement après feu.

4.8 La variabilité naturelle

Le paysage naturel de chacune des 14 unités homogènes observées sur le territoire a d'abord été défini en regard du cycle de feu actuel. Par ailleurs, afin de caractériser le paysage naturel de chacune des unités homogènes selon sa variabilité naturelle, nous avons eu recours aux études paléoécologiques réalisées sur le territoire d'étude. L'idée de base était d'associer une variabilité naturelle à chacun des vastes territoires couverts par les trois cycles de feu (Chapitre 3, figure 3.5). La variabilité présentée est très vaste (de 50 à 350 ans) et similaire à celle estimée par Cyr et al. (2009). Ces données ont été utilisées afin d'estimer la variabilité des divers stades évolutifs dans les diverses portions du territoire d'étude (Figure 2). Enfin, connaissant les limites de variabilité, nous avons statué sur le fait que cinq unités homogènes sortaient de leur variabilité naturelle. Quatre d'entre elles étaient considérées comme résilientes parce que le temps et les processus de dynamique forestière devraient conduire éventuellement au retour à des proportions de stades évolutifs et à une structure d'âge apparentés à ceux des paysages naturels. La cinquième, localisée à l'extrémité ouest du territoire, était considérée comme non résiliente en raison de l'impossibilité pour les nombreuses tremblaies d'évoluer vers des peuplements conifériens. Nous estimons que les vastes paysages dominés par des tremblaies à aulne issues de feux répétés et de coupes, ne peuvent évoluer vers des peuplements conifériens. Afin de confirmer cette hypothèse, des études de terrain seraient nécessaires, notamment afin de juger du potentiel de la régénération à former éventuellement une mosaïque forestière qui s'approche des paysages naturels.

Une interrogation qui peut être soulevée concerne le fait que la variabilité a été définie sans considérer les changements susceptibles de survenir au niveau des végétations potentielles au cours de l'échelle plurimillénaire. Une esquisse de ces changements est présentée à la figure 2. Ainsi, par exemple, certains peuplements aujourd'hui considérés comme appartenant à la végétation potentielle de la sapinière à bouleau blanc ont possiblement fait partie de la végétation potentielle de la sapinière à bouleau jaune lors de l'optimum climatique (8000 à 4000 ans AA). D'autres possibilités de modifications de végétations potentielles sont évoquées à la Figure 2.

Figure 2. États de référence pour les unités homogènes de la portion sud du territoire (4 unités homogènes). Les couleurs caractérisent les stades évolutifs de début (couleurs pâles) et de fin (couleurs foncées) de succession. Chacun des stades évolutifs est accompagné d'un écart-type basé sur la variablité naturelle des cycles de feu (chapitre 3, figure 3.5)



Présence de thuya, pin blanc, bouleau jaune lors de l'Optimum climatique. Perte de ces espèces depuis le début du néoglaciaire (4000 ans), et surtout depuis 2500 ans (boréalisation).

Possibilité de transition de RS2->RE2 depuis le début du néoglaciaire sous l'effet des feux.

Possibilité de transition de MS2->RE2 depuis le début du néoglaciaire sous l'effet des feux.

Possibilité de transition de RE2->RE3 depuis le début du néoglaciaire sous l'effet d'un climat plus humide.

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CONCLUSION GÉNÉRALE

Cette étude se veut une contribution à la connaissance de l'hétérogénéité paysagère contemporaine d'un vaste territoire (175 000 km^2) de la forêt boréale québécoise. Cette hétérogénéité, définie comme étant *le résultat de la complexité des paysages forestiers causée par les interactions entre la distribution spatiale des caractéristiques environnementales et les réponses différentielles de la végétation* (White 1979, Milne 1991, Legendre 1993, Wagner et Fortin 2005), a été analysée en considérant les concepts développés par plusieurs écologistes. Dans un premier temps, l'étude repose sur la notion des gradients écologiques (Whittaker 1967, Whittaker 1978, Richard 1995), gradients que nous avons définis à partir de la végétation ainsi que des principales familles de variables explicatives qui en influencent la distribution, notamment le climat, les perturbations naturelles, le milieu physique et les perturbations humaines (Daubenmire 1936, Jenny 1958, White 1979, Grimm 1984, Turner 1989, Gerardin et Ducruc 1990). Les gradients écologiques, le long desquels s'exprime l'hétérogénéité des paysages, ont par la suite été segmentés dans le but de connaître les spécificités locales de la végétation et de ses variables explicatives (unités homogènes) selon plusieurs niveaux de perception (Dufrêne et Legendre 1991, Dufrêne 1992, Grondin et al. 2007, 2014). Grâce aux développements de l'écologie numérique des 20 dernières années, la méthode d'analyse de l'hétérogénéité a été orientée vers l'estimation de la contribution des familles de variables explicatives qui causent la variabilité de la végétation (Borcard et al. 1992, Tuomisto et al. 2003, Legendre et al. 2005, Borcard et al. 2011, Dray et al. 2012). Bien que les perturbations humaines ne se soient pas avérées être une famille de variables dominante, elles ont cependant marqué la portion sud du territoire au cours des 100 dernières années. Dans ce contexte, et dans le but de soustraire de cette partie de l'analyse les effets des perturbations humaines pour mieux en cerner les autres influences, nous avons cherché à définir des paysages naturels et à les comparer aux paysages aménagés (Bergeron et Dansereau 1993, Leduc et al. 1995, Gauthier et al. 1996, Grondin et al. 2010). L'ensemble de la caractérisation de l'hétérogénéité vise finalement à apporter des connaissances utiles à la mise en place de l'aménagement écosystémique des forêts (Bergeron et Harvey 1997, Harvey et al. 2003, Gauthier et al. 2008, Raulier et al. 2009, Boucher et al. 2011). Nous avons donc tenté de décrire l'hétérogénéité des paysages (gradients écologiques), d'en déterminer les causes (écologie numérique), de la décomposer en cellules territoriales relativement similaires quant à leur contenu (unités homogènes) et de quantifier l'impact des activités anthropiques (comparaison des paysages naturels et des paysages aménagés). Nous avons finalement proposé que les paysages naturels obtenus d'un ensemble de processus écologiques (ex. cycle de feu), excluant les activités anthropiques, soient considérés comme des états de référence pour l'aménagement écosystémique.

Notre contribution à la connaissance de l'hétérogénéité paysagère s'articule autour de trois volets.

1- Le premier est que *l'hétérogénéité de la végétation des paysages est causée par des changements simultanés de quatre familles de variables explicatives (climat, perturbations naturelles, milieu physique, perturbations humaines) survenant le long des gradients écologiques; la contribution des perturbations humaines est moindre que celle des familles naturelles, mais elle demeure significative. De plus, l'hétérogénéité des paysages, définie par des gradients écologiques, varie selon le thème de végétation (espèces forestières, types forestiers, végétations potentielles-stades évolutifs).*

   C'est ainsi que deux types d'hétérogénéité des paysages ont été mis en évidence. Le premier type considère le thème des espèces forestières ainsi que le thème des végétations potentielles-stades évolutifs; les variables descriptives de la végétation ainsi que les variables explicatives présentent des gradients écologiques et des structures spatiales épousant principalement le gradient latitudinal. Le second type d'hétérogénéité caractérise le thème des types forestiers. Dans ce cas, la variation de la végétation expliquée par les perturbations naturelles et le climat est à peine supérieure à celle du milieu physique. Le milieu physique est donc plus important que sous les thèmes précédents. Également, le gradient latitudinal-oblique joue un rôle important dans la répartition de la végétation lorsque les types forestiers sont considérés. Ce gradient s'exprime principalement depuis le sud-est vers le nord-ouest du territoire, soit dans le sens d'une végétation d'abord bien pourvue en sapin dans les reliefs de collines, puis vers les tourbières non forestières ou dominées par l'épinette noire. Peu importe le type d'hétérogénéité, la combinaison des familles de variables explicatives contribue toujours à expliquer une variation importante de la végétation. Dans tous les cas, la variation expliquée par les perturbations humaines demeure encore relativement faible.

Ce volet de l'étude apporte également d'autres nouveaux éléments.

- Il démontre que l'hétérogénéité paysagère est largement causée par l'intégration ou la combinaison de plusieurs familles de variables explicatives. Cette démonstration repose sur une description de l'hétérogénéité se situant à l'échelle du paysage (district écologique) et intégrant autant les perturbations naturelles que les perturbations humaines. La démonstration s'appuie sur un cheminement méthodologique défini par l'écologie numérique, et cela permet 1) d'établir des liens entre, d'une part, les gradients écologiques et, d'autre part, les structures spatiales (cartes) caractérisant autant les thèmes de végétation que les familles de variables explicatives, 2) et de quantifier la variation de la végétation expliquée par les familles de variables explicatives, seules (uniques) ou en combinaison avec les autres.

- Ce premier volet démontre également que l'hétérogénéité paysagère est structurée (fort pourcentage de variation expliquée). Si ce n'était le cas et que l'hétérogénéité était désorganisée, il serait impossible de définir des gradients écologiques ainsi que des structures spatiales, et de quantifier leur chevauchement. Nous estimons donc que les variables environnementales et les niches écologiques sont des éléments importants dans la répartition de la végétation. Nous considérons que les résultats obtenus dans cette étude pourraient être extrapolés à l'ensemble de la forêt boréale, les mêmes facteurs s'y trouvant à l'oeuvre. L'intégration devrait être une constante; elle devrait s'appliquer à la majorité des biomes, autant terrestres qu'aquatiques. Par exemple, Thiffault et al. (sous presse) se sont intéressés aux relations entre les éricacées et les variables explicatives dans la forêt boréale québécoise et leurs résultats appuient le paradigme de l'intégration. Par ailleurs, l'importance des familles devrait varier selon les processus écologiques qui gouvernent la répartition de la végétation. Dans les endroits moins affectés par les perturbations naturelles que notre territoire d'étude, le milieu physique pourrait s'avérer la famille dominante. Ces nuances se perçoivent dans l'étude de Grondin et al. (2007) portant sur le partitionnement de la variation de la végétation à l'échelle du Québec méridional.

2- Le second volet de la contribution de ce travail à la connaissance de l'hétérogénéité paysagère est que, *puisque cette hétérogénéité est décrite par le chevauchement de groupes de variables de végétation et de groupes de variables explicatives le long des gradients écologiques, il est possible de scinder ces gradients selon une hiérarchie d'entités géographiques toujours plus petites et similaires (unités homogènes) au regard de la végétation et de ses variables explicatives.*

Dans cette section, l'hétérogénéité des paysages telle que définie par des gradients écologiques a été segmentée en cellules relativement homogènes. Ces cellules sont agencées de façon à former une classification hiérarchique définie par trois niveaux de perception *d'unités homogènes de végétation.* Le premier niveau permet de distinguer les deux domaines bioclimatiques du territoire d'étude. Au second niveau, le territoire est subdivisé en trois grandes entités. La première est associée aux épidémies de tordeuse des bourgeons de l'épinette (portion sud), la seconde, aux peuplements de début de succession (pinèdes grises et tremblaies) relativement jeunes (surtout dans la portion centrale) et la troisième, aux peuplements de fin de succession (principalement des pessières noires) relativement âgés (prédominant dans la portion nord). Le dernier niveau, le plus détaillé, est composé de 14 unités homogènes. Quelques-unes sont affectées depuis près de 100 ans par les activités anthropiques (feux d'origine humaine, coupe), ce qui a favorisé le développement des feuillus de lumière (peuplier faux-tremble, bouleau à papier). Enfin, le partitionnement de la variation de la végétation pour l'ensemble du territoire ainsi que sur diverses portions (sapinière, pessière, extrémité ouest du territoire) révèle qu'une part importante de la variation de la végétation est expliquée par la combinaison des familles de variables explicatives. Ces résultats confirment que le paradigme de l'intégration se manifeste à plusieurs niveaux de perception, soit à l'échelle médiane (*mesoscale*, notre territoire d'étude), mais vraisemblablement aussi à l'échelle supérieure (*macroscale*), qui fait référence à des territoires plus vastes que celui à l'étude (ex. : l'ensemble du Québec méridional, Grondin et al. 2007) et à l'échelle inférieure (*microscale*), qui caractérise plus finement les paysages à l'échelle de la toposéquence. Cette dernière projection devrait cependant être validée par des études faites à ce niveau.

Les éléments nouveaux apportés par ce volet touchent également plusieurs autres aspects.

- D'abord un système de classification formé de plusieurs niveaux de perception (hiérarchie) et qui intègre, à priori, les perturbations naturelles et humaines, a été élaboré. Cette démarche diffère des études précédentes où les perturbations naturelles, lorsque considérées, venaient se superposer à un système de classification reposant sur le climat et le milieu physique.

- Ensuite, une typologie d'unités novatrices dans le domaine de la classification écologique du territoire a été mise en place; ces unités sont novatrices parce qu'elles sont le reflet du concept d'intégration des familles de variables explicatives dominé par les perturbations naturelles. Ces unités montrent des affinités avec la classification des mosaïques forestières de Turner et al. (1993) relativement à leur stabilité et leur équilibre.

- Également, on a identifié la présence d'unités homogènes (n = 5) où les activités anthropiques jouent un rôle de premier plan dans le développement de la végétation.

- En dernier lieu, on a démontré que la variation de la végétation causée par plusieurs familles de variables explicatives s'applique à plusieurs échelles de perception (*macroscale, mesoscale*); le paradigme de l'intégration est donc multi-échelles.

3- Après un premier apport qui définissait les bases de l'analyse de l'hétérogénéité des paysages en s'appuyant sur les gradients écologiques spécifiques à trois façons de décrire la végétation, et après le second qui procédait à l'élaboration d'une typologie des paysages basée sur l'intégration des processus écologiques, le troisième volet a consisté à mettre en lumière des éléments visant à *bonifier notre connaissance de l'hétérogénéité des paysages par une analyse plus approfondie qu'auparavant des activités anthropiques. Ces dernières modifient les paysages naturels, au point que les unités homogènes fortement touchées (paysages* *aménagés) présentent des écarts importants de structure et de composition avec les paysages naturels.*

Ce troisième élément repose sur l'estimation des caractéristiques d'un paysage naturel pour chacune des 14 unités homogènes du vaste territoire d'étude ainsi que sur une analyse des écarts avec les paysages aménagés. Les résultats montrent que la majorité des unités homogènes sont caractérisées par un cycle de feu relativement court (130-160 ans), environ 45-50 % de forêts de plus de 100 ans et par environ 60 % de peuplements de fin de succession. Dans la majorité des paysages aménagés (10 sur 14), la proportion de forêts de plus de 100 ans n'est plus que de l'ordre de 10-15 %, comparativement au paysage naturel. De plus la proportion de peuplements de fin de succession, appartenant à diverses végétations potentielles, a chuté de façon marquée. Finalement, cinq unités homogènes sont considérées comme étant à l'extérieur de leur variabilité naturelle en raison de plus d'un siècle d'activités anthropiques, notamment la coupe forestière et les feux d'origine humaine (feux de colonisation). La majorité de ces unités sont cependant considérées comme résilientes. Cette conclusion va dans le sens de celles de nombreux travaux réalisés dans d'autres régions touchées par les activités anthropiques (Urban et al. 1987, Lorimer 2001, Grondin et Cimon 2003, Grondin et al. 2014, Laquerre et al. 2009).

Les apports originaux de ce dernier volet portent sur trois points.

- Le premier consiste en l'élaboration et l'utilisation d'une méthode d'estimation du paysage naturel d'unités territoriales homogènes sur la base des cycles de feu, de la structure d'âge et de la modélisation de la dynamique forestière. La méthode et les résultats qui en découlent sont applicables à de vastes territoires. De là, il est possible de cibler des enjeux plus précis pouvant faire l'objet de travaux ultérieurs.

- Le deuxième point est formé par la prise en compte d'une variabilité naturelle qui couvre d'abord la période contemporaine (200-300 dernières années), ce qui permet de considérer les changements dans les cycles de feu liés au Petit Âge Glaciaire. De plus, la prise en compte de la variabilité s'étend sur tout le reste de l'Holocène.

- Enfin, le troisième point cible le fait que les paysages naturels, caractérisés par une variabilité spatiale contemporaine et plurimillénaire, peuvent être considérés comme des états de référence pour l'aménagement écosystémique.

Implications de l'étude dans la mise en oeuvre d'une stratégie écosystémique et perspectives futures

Le développement d'une stratégie d'aménagement forestier s'inspirant de la dynamique des paysages naturels comprend principalement trois étapes (Bergeron et Harvey 1997, Harvey et al. 2003, Raulier et al. 2009) : la première consiste à reconstituer le régime des perturbations naturelles, la deuxième vise à étudier l'évolution à long terme de la structure et de la composition des peuplements à la suite des perturbations, et la dernière étape consiste à développer des interventions sylvicoles respectueuses de la dynamique naturelle des perturbations. À la suite de notre analyse, il apparaît essentiel de définir l'hétérogénéité d'un territoire à partir de l'ensemble des variables susceptibles de la créer, notamment le climat, les perturbations naturelles, le milieu physique et les perturbations humaines, car seule la prise en compte de la totalité des forces écologiques en présence peut garantir l'efficacité maximale des moyens d'intervention utilisés. Il est également proposé de modifier légèrement les étapes de la stratégie d'aménagement afin de l'adapter à de vastes teritoires, à l'exemple de celui considéré dans cette étude. Les étapes proposées seraient donc :

1- de caractériser le territoire d'étude relativement à la végétation et à ses variables explicatives (gradients écologiques : climat, perturbations naturelles et humaines, milieu physique);

2- sur la base de gradients écologiques, de définir des unités homogènes de végétation en tenant compte de leur degré d'altération par les activités anthropiques;

3- de caractériser chacune des unités de territoire selon son cycle de feu; autant que possible, considérer les cycles de feu actuels et passés de façon à couvrir le maximum de variabilité holocène;

4- de décrire la dynamique forestière, selon un système exprimant la dynamique de la végétation : les végétations potentielles et les stades évolutifs, ou les cohortes;

5- de définir un paysage naturel pour chacune des unités homogènes en intégrant les connaissances sur les cycles de feu, les structures d'âge à l'échelle du paysage et la dynamique forestière;

6- de comparer les paysages naturels et les paysages actuels (analyse d'écarts) afin d'identifier les unités les plus touchées par les activités anthropiques;

7- et, en dernier lieu, de définir des stratégies sylvicoles appropriées afin de réduire les écarts entre les deux types de paysages.

Cette étude s'est donné comme but d'établir un modèle d'analyse qui rende plus cohérente la description de l'hétérogénéité spatiale d'un vaste territoire de la forêt boréale, en insistant sur l'action simultanée et complémentaire de plusieurs familles de variables explicatives. Les perturbations naturelles et humaines se sont révélées y occuper une place majeure et ont démontré leur complémentarité au climat et au milieu physique. À la suite des conclusions de notre analyse, des efforts devraient être déployés afin de caractériser plus finement les processus écologiques à la base du développement des paysages aménagés, à l'exemple de l'enfeuillement noté dans plusieurs unités homogènes touchées par les activités anthropiques. De plus, l'acquisition de connaissances sur les liens entre des paysages naturels décrits à partir de la végétation contemporaine, comme ce fut le cas dans cette étude, et des paysages naturels décrits sur la base de la paléoécologie (ex. analyse des sédiments lacustres) devrait être encouragée en ayant comme objectif de dégager, par des méthodes distinctes, les spécificités des divers paysages (unités homogènes) et des milieux écologiques qui les composent (végétation potentielle) au regard de leur histoire Holocène. Enfin, estimer l'évolution des paysages sous l'effet des changements climatiques et la comparer à l'évolution naturelle actuelle et passée demeure un défi intéressant à relever (Terrier et al. 2013).

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